

The structure and affinities of the Hedyloidea: a new concept of the butterflies

M. J. Scoble

Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The affinities of the Hedylidae, a group of about 40 Central and South American Lepidoptera, are reassessed. Currently, the taxon is treated as a tribe ('Hedylcae') of the Oenochrominae (Geometridae), but evidence is presented here to show that hedyliids are butterflies although they look moth-like in many respects. The five generic names in the family are synonymized in this work with the oldest, *Macrosoma* Hübner.

The taxonomic history of the Hedylidae is discussed, and the reasons for the proposed assignment of the family to the Rhopalocera are given. A description of the family is followed by comments on characters selected for their biological or systematic interest. In this section comparisons are made between the Hedylidae and other Lepidoptera, particularly the butterflies, and their phylogenetic relationships are discussed. Hedylidae + Hesperioidea + Papilionoidea (s.str.) probably form a monophyletic taxon, although doubts have been expressed about the relationship between skippers and true butterflies. It is tentatively suggested that within the Rhopalocera, the Hedylidae are more closely related to the Papilionoidea than are the Hesperiidae to the Papilionoidea; that is, the butterflies without the Hedylidae are paraphyletic.

The evidence of the butterfly affinities of hedyliids comes from adults, larvae, and pupae; the structure of the thorax and the base of the abdomen of the adult was found to be particularly revealing.

Key words: Lepidoptera, Rhopalocera, Hedyloidea *stat. n.*, Hedylidae, Geometridae, morphology, phylogeny.

Introduction

Guenée (1857) described the Hedylidae as one of the 26 component families of the Phalénites. The Phalénites are, with modification, the equivalent of what are now called the Geometridae. The Hedylidae were treated by Prout (1910; 1931) as a tribe ('Hedylcae') of the Oenochrominae (Geometridae), and no reassessment of the relationships of the group has been attempted subsequently. In fact the Hedylidae are misplaced in the Geometridae, the most obvious reason being the absence of tympanal organs from the base of the abdomen in the former – structures that are characteristic of the latter.

The Hedyliidae consist of some 40 species, from South or Central America. Below, I argue that not only is this group misplaced in the Geometridae but also that its phylogenetic affinities are with the butterflies (Rhopalocera: Hesperioidea or skippers, and Papilionoidea or true butterflies) despite the moth-like external appearance of the adult insects.

Both Guenée (1857) and Prout (1910; 1931) noted certain similarities between hedyliids and butterflies. Guenée even went so far as to name one species *napiaria* because it resembled the pierid butterfly *Pieris napi* (L.). He named another species *heliconiaria* since it reminded him of certain species of the papilionoid genus *Heliconius* Kluk. Prout (1910; 1931) noted the butterfly-like shape of the adults, and the remarkable girdled pupa in the two species for which he had information. However, neither of these workers suggested that these features meant that hedyliids and butterflies were related, and they presumably regarded the similarities as independent derivations. Prout (1931) was clearly uncomfortable about the geometrid affinities of the group since he suggested that the 'Hedylidae' might deserve even a separate family status. However, neither he nor Guenée apparently considered that the butterfly-like features they observed might actually be homologous in the taxa concerned and thus indicative of true affinity. Why?

There are two reasons, one philosophical and one practical. We tend to develop a conception of a given taxon. We think of butterflies as a package, and develop what might be termed a butterfly *Gestalt* – colourful, diurnal lepidopterans with clubbed antennae and amplexiform rather than frenate wing-coupling. This is not to say that we do not recognize *exceptions*. Males of the skipper *Euschemon* Doubleday have a frenulum and retinaculum; satyrines generally are not brightly coloured, many butterflies do not have strongly clubbed antennae, and a few are nocturnal. By definition, exceptions do not destroy a *Gestalt*. But hedyliids do not conform to the traditional butterfly package. They do not have clubbed antennae; in some species these structures are even bipectinate. In males of most species the frenulum and retinaculum are very well developed, and the wing pattern in most species bears little resemblance to that of butterflies (Figs 1–18). Most species seem to be nocturnal.

Most taxa are diagnosed by a *set* of attributes rather than by a single character or very few characters. Even so, such diagnoses often need qualification to incorporate those taxa that do not fit – for example, primitive species that have not yet acquired all the attributes of the majority, or those specialized species that have lost them secondarily. Crowson (1970), noting the essentialist nature of such diagnoses, called the groups Aristotelian to distinguish them from taxa delimited phylogenetically. Crowson also coined the phrase 'the non-congruence principle' to suggest that it is most unlikely that a taxon can be defined on more than one or two characters, since when a taxon originates many of the characters found in later members of the group have not yet evolved. Characters we regard as typical of a given taxon do not evolve at once. Therefore, in the present case, we should not expect the ground plan of the butterflies as a whole or even the true butterflies to exhibit the characteristics of the more advanced members of the group. It should not, then, be unexpected to find a group strongly affiliated to the butterflies that does not fit our conception of them. However, if it is our stated aim to produce, as far as possible, a phylogenetic classification, then merely one derived character shared between two taxa provides evidence of monophyly. In fact, the Hedyliidae possess several such characters.

Having rejected the idea that hedyliids might be related to butterflies, neither Guenée nor Prout looked further. This may largely have been because morphological studies were less extensive in Guenée's time than they are today. Much the same can be said of Prout, who had a remarkable ability to observe structures and their significance on dried specimens, but did little dissection. (Only late in his career did he study genitalia.) In fact many of the characters that support the suggestion that hedyliids are butterflies are to be observed only after detailed examination of the sclerites of the thorax and the base of the abdomen.

The present study evolved from a project to re-diagnose the Oenochrominae (Geometridae), and to exclude those groups that currently make the subfamily unnatural (non-monophyletic). The extraordinary combination of attributes of the Hedyliidae demonstrates that their affinities lie neither with *Oenochroma* Guenée (the type genus of the Oenochrominae) and its relatives, nor with the Geometridae as a whole. In particular, abdominal tympanal organs, which are

typical of geometrids, are absent from hedyliids. Also, prolegs are present on abdominal segments 3 to 6 and 10 of the larva, unlike most geometrids where their number is reduced. The first tergum of the abdomen is strongly 'pouched' (a condition described for papilionoids by Ehrlich, 1958b), and pre- and postspiracular bars are present. The abdomen is curved and flattened laterally, particularly in the male. The remarkable pupa is attached to a leaf by a silken girdle: there is no cocoon. The apical tibial spurs of the hindleg are absent in all species except the male of one. The precoxal (or paracoxal) sulcus of the mesothorax joins the 'marginopleural' sulcus. In the metathorax the furcal apophysis is weakly sagittate in dorsal view. The pretarsus is lost from the forelegs of the male although minute claws are present, and the tarsomeres are reduced to two by fusion. The head of the larva is extended into a pair of extremely long horns, and there is an anal comb on abdominal segment 10. These characters are all represented in various butterflies. In contrast, the moth-like features include the absence of clubs on the antennae, and a well-developed frenulum and retinaculum in the males of most species, although they are reduced and functionless in a few. The wing venation is peculiar: Rs_3 and Rs_4 share a common stem, but Rs_2 is separate from the cell and is not stalked with Rs_3 . Rs_1 and Rs_2 are distinctly sinuate. Special modifications of the wings, including a complex of small chambers at the base of the forewing and a prominent flap extending from Sc , are described below.

The body of this work aims to provide the evidence that suggests that hedyliids are butterflies. Are the apparent butterfly attributes genuinely shared-derived characters of hedyliids and butterflies or are they convergent or parallel developments? In short, are the Hedyliidae more closely related to the butterflies than to any other lepidopterans?

A further question is: are the Hedyliidae more closely related to the true butterflies (Papilionoidea) than to the skippers (Hesperioidea), or does the family represent the sister group of the Rhopalocera as a whole?

A general description of the characters found in this family is provided, together with a summary of its biology and distribution. This is followed by observations on selected structures with comments on their systematic importance. Finally, the evidence for the affinity of the Hedyliidae with the Hesperioidea and the Papilionoidea is assessed.

Material

The observations were based on specimens housed in the British Museum (Natural History). Juvenile stages of one species were lent by Mr R. O. Kendall, San Antonio, Texas.

Examination of the structure of the thorax was necessarily limited to avoid breaking up numerous specimens. From the study of more easily observed characters the family Hedyliidae appears to be a homogeneous group, and thoracic structures probably do not differ significantly between species. Thoracic structure was examined in species that showed most structural variation in the genitalia.

HEDYLIDAE Guenée

Hedyliidae Guenée, 1857: 521. Type genus: *Hedyle* Guenée, 1857: 521.

Guenée (1857) described the family for three genera, *Hedyle* Guenée, *Venodes* Guenée, and *Phellinodes* Guenée. With the exception of Prout (1910; 1931), most authors have been content to describe new species or genera without discussing the taxonomic relationships of the group as a whole. Prout, in both these works, dealt with all the genera and species. He treated the taxon as a tribe – the 'Hedylidae' – of the subfamily Oenochrominae (Geometridae). Authors who preceded Prout assigned the genera to various infrafamilial categories of the Geometridae, some of which are not currently in use, with no justification for their action. Kendall (1976), in his notes on the life-history of one species, used the name Hedyliidae, therefore effectively reviving Guenée's original status.

The use of the name Hedyliidae is fully justified by Guenée's priority, Kendall's subsequent usage, and the absence of any competing name.

Generic synonymy

The species of the family show no fundamental structural difference from each other, and form a highly compact group, particularly in the male genitalia, wing venation, wing shape, legs and antennae. Below, I synonymize the five genera that are currently accepted. Three of these are monotypic.

Macrosoma tipulata Hübner and *Lasiopates hyacinthina* Warren are species that exhibit the greatest differences from the majority of the family. The valvae of the male genitalia of *hyacinthina* (Fig. 79) are of a more complex shape, the two components of the gnathos are not fused medially, and the juxta is characteristic.

One reason for the proliferation of genera in the Lepidoptera is that since the study of the male genitalia became universal, there has been a strong tendency to treat as genera those groups where there is a morphological 'gap' in these structures. The consequence has been that although a family may contain a few large genera there are usually several anomalous species. If these are then excluded from one of the main genera each has to be assigned to a new genus. In a family with several large genera it may be impossible to decide to which genus such 'outlier' species should be assigned. The description of a new genus therefore becomes inevitable. In a family with one large genus there is often a good case to be made for including all species within that genus and using lower categorical rank, e.g. subgenus, or simply species-group, to distinguish outliers. In the present case, despite the synonymy, I have not so divided *Macrosoma* in this way. This is best left until such time as a revision of all the species is undertaken. The synonymized names can then be used as subgenera, if required.

MACROSOMA Hübner

Epirrita Hübner, 1808. [Name unavailable, see Fletcher, 1979.]

Macrosoma Hübner, 1818: 10. Type species: *Macrosoma tipulata* Hübner, 1818: 10 (by monotypy).

Hedyle Guenée, 1857: 521. Type species: *Hedyle heliconiaria* Guenée, 1857 (by monotypy). [Four described species.] **Syn. n.**

Venodes Guenée, 1857: 522. Type species: *Venodes napiaria* Guenée, 1857: 522 (by monotypy). [Monotypic.] **Syn. n.**

Phellinodes Guenée, 1857: 523. Type species: *Phellinodes satellitiata* Guenée, 1857: 523 (by monotypy). [Thirty-three described species.] **Syn. n.**

Macrophila Walker, 1862: 1463, 1465. Type species: *Macrosoma tipulata* Hübner, 1818 (by monotypy). [Junior objective synonym of *Macrosoma*, see Fletcher, 1979.]

Hyphedyle Warren, 1894: 375. Type species: *Hedyle rubedinaria* Walker, 1862: 1464 (by original designation). [Synonymized with *Hedyle* Guenée by Prout, 1910.]

Lasiopates Warren, 1905: 310. Type species: *Lasiopates hyacinthina* Warren, 1905: 311 (by original designation). [Monotypic.] **Syn. n.**

Hedylidae remains the valid name of the taxon since family names are not rejected when, after 1960, their type genera are found to be junior synonyms.

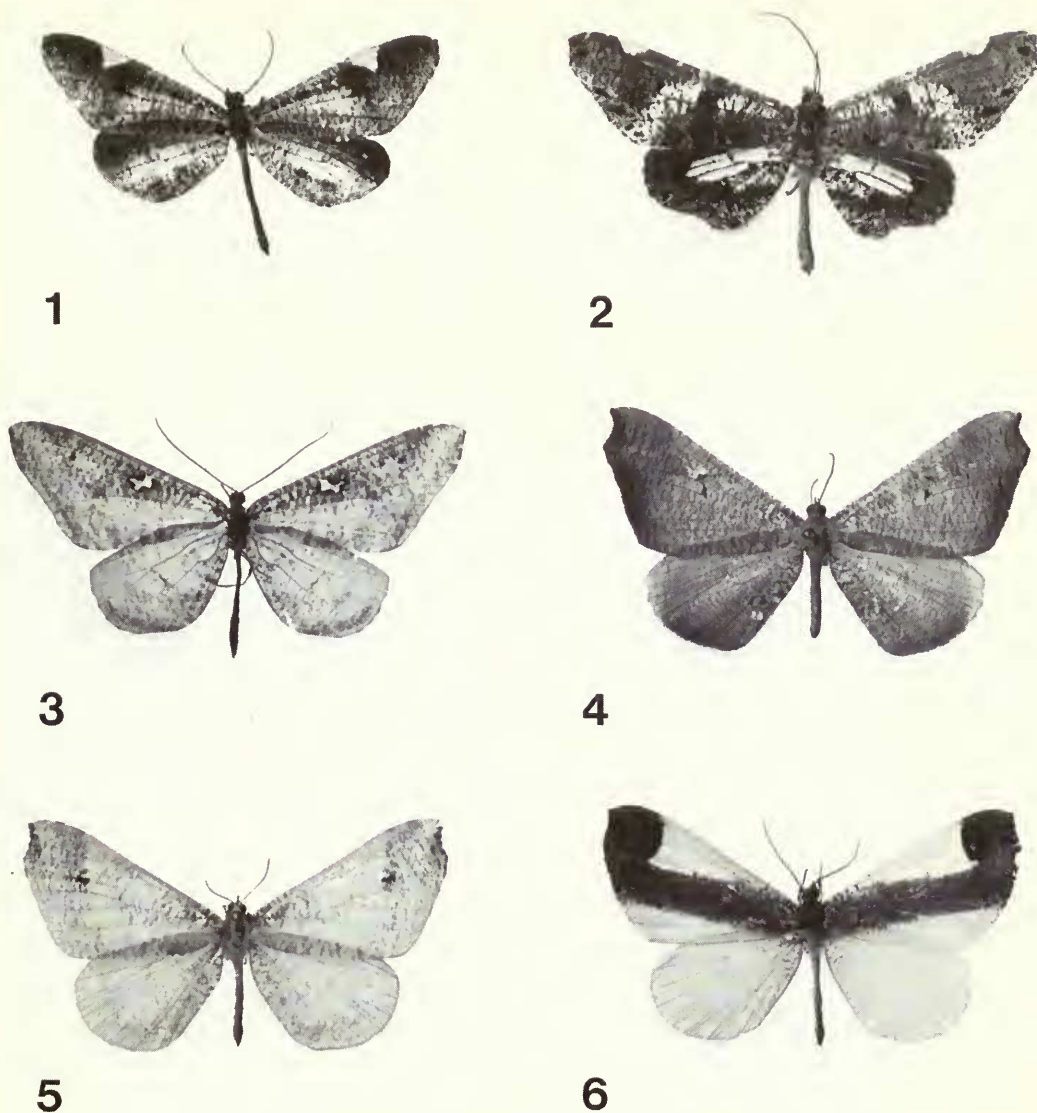
General appearance

Hedylids are fairly delicate insects with curved abdomens, particularly in the male (Fig. 63). Figs 1–18 show the main variation in wing patterns: many of the species bear semi-transparent patches on the wings. The fore wings are weakly or strongly emarginate at the apex. The larva (Figs 19, 100, 101) bears a pair of very long 'horns' on the head capsule, prolegs on abdominal segments 3 to 6 and 10, a pair of furcae on the anal segment, and an anal comb. The pupa (Figs 20, 21) lacks a cocoon, and is attached to its substrate by a silken girdle.

Description

Adult

Head (Figs 22–29). Frons narrow and protuberant (Figs 22, 23). Compound eyes large. Ocelli absent. Chaetosemata present, one chaetosema behind each eye (Fig. 22). Antenna (Figs 25–28): bases close



Figs 1–6 Adults of Hedylidae. 1, *Macrosoma heliconiaria* (Guenée), $\times 1.5$; 2, *M. hyacinthina* (Warren), $\times 1.1$; 3, *M. tipulata* Hübner, $\times 1.1$; 4, *M. rubedinaria* (Walker), $\times 1.5$; 5, *M. ustrinaria* (Herrich-Schäffer), $\times 1.5$; 6, *M. leucophasiata* (Thierry Miege), $\times 1.5$.

together; filiform (Figs 26, 27) or bipectinate (Fig. 25); scaled dorsally. Pilifers present. Maxillae: palpi minute, one-segmented; galeae form a well-developed proboscis, not scaled at base. Labial palpi ascending (Fig. 24), three-segmented with a deep sensory invagination on distal segment (Fig. 29). Tentorium: medial swelling on each tentorial arm (Fig. 23), but dorsal arms not developed.

Thorax (Figs 30, 31). Prothorax with membranous patagia and parapatagia; patagia protuberant. Mesothorax: anepisternum well developed, not reduced (Fig. 30); precoxal sulcus (paracoxal sulcus of Scott, 1985) joins 'marginopleural' suture (Fig. 31). Metathorax: furcal apophyses weakly sagittate in dorsal view; dorsal lamellae of secondary furcal arms fused mesally in their extension anteriorly from the arms to the furcal apophyses.

Wing venation (Fig. 32). (Following the recommendations of Wootton (1979), in this work I label the



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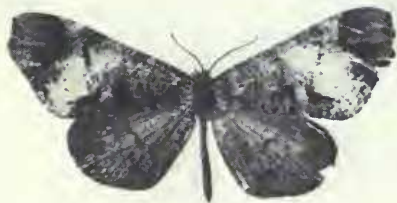
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Figs 7–12 Adults of Hedyllidae. 7, *Macrosoma subornata* (Warren), $\times 1.5$; 8, *M. paularia* (Schaus), $\times 1.5$; 9, *M. coscoja* (Dognin), $\times 1.5$; 10, *M. satellitiata satellitiata* (Guenée), $\times 1.1$, hyaline patch arrowed; 11, *M. albifascia albifascia* (Warren) $\times 1.1$; 12, *M. hedyllaria* (Warren), $\times 1.1$.

branches of the radial sector as Rs_1 , Rs_2 , etc., to distinguish them from the radius (R_1).) Fore wing: accessory cells absent. Rs_1 and Rs_2 sinuous after branching from cell; Rs_4 stalked with Rs_3 , Rs_2 not stalked with Rs_3 (although it shares a common stem with Rs_3 and Rs_4 before the three branches arise); Rs_4 remote from M_1 ; CuP often weakly indicated; M_2 about equal distance from M_1 as from M_2 ; anals forked at base. Hind wing: Rs separate from $Sc+R_1$ from near base of wing; M_2 about equidistant from M_1 and M_3 .

Wing coupling (Figs 33–37). Male usually with strong frenulum and a very long, well-developed retinaculum; frenulum occasionally reduced and non-functional (Fig. 35). Female: frenulum composed of a few bristles (Fig. 36); retinaculum absent.

Wings: pattern and specializations. Figs 1–18 illustrate the variety of shape and pattern. Vestiture: rather weakly scaled; prominent piliform scales present particularly near base of wings (Fig. 38), and more



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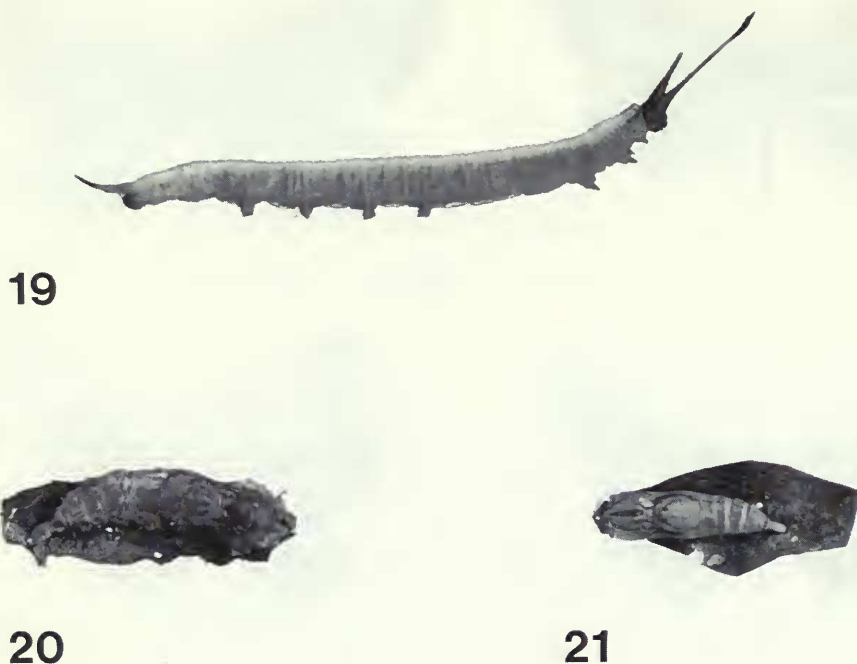
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Figs 13–18 Adults of Hedyllidae. 13, *Macrosoma lucivittata* (Walker), ♂, $\times 1.1$; 14, *M. lucivittata* (Walker), ♀, $\times 1.1$; 15, *M. nigrimacula* (Warren), $\times 1.1$; 16, *M. leptosiata* (Felder), $\times 1.1$, hyaline patch arrowed; 17, *M. napiaria* (Guenée), $\times 1.1$; 18, *M. hedyllaria* (Warren), ventral surface with wings folded vertically, $\times 1.5$.

numerous on hind wing than fore wing. Upperside and underside with the same pattern. Areas of semi-transparent scales often present. *Fore wing* long, not broad, weakly falcate often with apex weakly emarginate; posterior edge expanded into a small lobe at base of wing in males of some species (Fig. 43), sometimes merely a very weak expansion. Holding area (*Haftfeld*) not present on ventral surface (nor on metascutum). Two small, but prominent chambers at base of wing (Figs 37, 42); one, predominantly in the



Figs 19–21 Larva and pupa of Hedyliidae. 19, larva of *Macrosoma heliconiaria* (Guenée), $\times 3.5$; 20, 21, pupal exuviae of (20) *M. lucivittata* (Walker), $\times 1.5$; (21) *M. nigrimacula* (Warren), $\times 1.5$.

ventral plane, is a distension of base of *Sc*, the other, predominantly in the dorsal plane, a distension of *Cu*. Prominent ventral fold expands from *Sc* on underside (Figs 39, 40). Scale-enclosed pocket present at very base of underside of wing (Figs 40, 41). *Hindwing* rounded: in males often with folded area (of glassy appearance) present (Figs 10, 16, 44, 47); basally usually with associated sclerotized protuberances (Figs 44–47, 50) and specialized scales (Figs 48, 49); base of costa weakly or, when frenulum is reduced, strongly expanded into a 'shoulder' (Fig. 35), composed of extended frenulum-plate and costal region.

Base of fore wing (Figs 37, 51). Second median plate with substantial part hidden under base of anal veins.

Legs (Figs 52–62). Microtrichia present on ventral surface at base of tarsi of mid leg and hind leg of male and all legs of female.

Fore leg. Epiphysis present (Figs 52–54); tibial spurs absent. Male: tarsus (Figs 52, 55, 57, 58) two-segmented, number reduced by fusion but tarsus not shortened; pretarsus reduced to pair of minute claws (Fig. 58), empodium and pulvilli absent; tarsi not spined, but hairy; occasionally with a scent brush. Female: tarsomeres not fused, tarsi five-segmented (Fig. 54); pretarsus not reduced, bears a pair of strongly curved claws (Fig. 59) that are weakly and asymmetrically forked; pulvilli present; tarsus spined ventrally, not hairy.

Mid leg: with one pair of tibial spurs; tarsus five-segmented, tarsomeres not fused; pretarsus not reduced, tarsal claws weakly forked; tarsus spined on ventral surface.

Hind leg: with one pair (Fig. 61) or occasionally two pairs (Fig. 62) of tibial spurs; tibia somewhat swollen; otherwise as mid leg.

Abdomen. Weakly to moderately curved (Fig. 63), flattened laterally not dorso-ventrally, and narrowing slightly towards base. Tympanal organs absent.

Pregenital abdomen (Figs 64, 65, 68). Segment I with narrow prespiracular bar and broad postspiracular bar (tergopleural). Tergum I with large membranous pouch and strong tergal braces. Sternum II with pair of mediolateral sclerotizations anteriorly; sternal apodemes reduced.

Male postabdomen (Figs 66, 67). Tergum VIII longer than sternum VIII forming a short hood.

Female postabdomen. Segment VII in form of a short hood over the genitalia; tergum VII large; sternum VII shorter, usually bearing a series of prominent setae on fold just anterior to the ostium bursae (Fig. 90).

Male genitalia (Figs 69–80). Genital capsule is 'deep' dorso-ventrally owing to length of lateral arms of vinculum. Segment IX comprises a completely sclerotized ring, i.e. tergum and sternum fused. Tegumen narrow, sometimes prominently bilobed. Uncus large, usually triangular in ventral view since it narrows apically; alternatively apex is truncated or otherwise modified (Fig. 83). Vinculum: ventral plate narrow and produced into a prominent narrow saccus; rarely, saccus is rounded. Gnathos usually large and heavily sclerotized; occasionally lateral arms do not meet medially. Valvae (Figs 77–82) simple, undivided, usually approximately triangular. Diaphragm unsclerotized, or occasionally sclerotized as a juxta into a small simple plate or, rarely, a prominent U-shaped structure (Fig. 84). Aedeagus (Figs 85–89) a simple tube; vesica unmarked, or with weak sclerotizations.

Female genitalia (Figs 90–99). Tergum VIII a well-sclerotized band. Anal papillae usually in form of a pair of ear-like lobes. Anterior apophyses sometimes reduced (Figs 93, 96). Posterior apophyses developed normally. Bursa copulatrix: a narrow ductus leads into a globose or sub-globose corpus; signum absent or present; if present then of a characteristic shape (Figs 98, 99).

Egg

An egg, found while dissecting the female genitalia of a specimen, was oval.

Larva

Based on *M. heliconiaria* (**comb. n.**) (Fig. 19, and see Kendall, 1976), with further information on *M. nigrimacula* (Warren) (**comb. n.**) derived from larval exuviae housed in the British Museum (Natural History). When this study was at an advanced stage, Mr T. Fox (London Butterfly House) provided a colour transparency of a larva (subsequently reared through) of *M. cascaria* (Schaus) (**comb. n.**), which he collected in Monte Verde, Costa Rica.

Head. Head-capsule bears a pair of long horn-like processes, flattened and broad in *heliconiaria* (Fig. 100), not broad in *nigrimacula* (Fig. 101). (Tips of processes out of focus in transparency of *cascaria*.) Hypognathous. Mandibles toothed. Six ocelli present. Secondary setae present.

Thorax and abdomen. Not pigmented. Secondary setae on dorsum capitate in *heliconiaria*, shorter and trifurcate in *nigrimacula*; row of knobbed setae run along midline in *heliconiaria*, absent from *nigrimacula*. Scoli absent. Primary setae not on pinaculi. True legs well developed, each bearing a single claw. Prolegs present on abdominal segments III to VI, and on X (Fig. 19). Plantae of ventral prolegs with crochets biordinal and uniserial; arranged in two transverse bands in *heliconiaria* and in a penellipse in *nigrimacula*. Abdominal segment X: anal plate extended into a pair of furcae; anal comb present.

Pupa (Figs 20, 21)

Known for five species (*heliconiaria*, notes and illustrations by Kendall (1976), and personal examination; *tipulata*, exuvial remains; *M. lucivittata* (Walker) (**comb. n.**), *nigrimacula*, and *cascaria* (well-preserved pupal exuviae).

The pupa is rather flattened, although raised protuberances arise from the thorax of *heliconiaria*, *lucivittata*, and *nigrimacula*, and from the abdomen of *lucivittata*, *nigrimacula*, and *cascaria*.

The pupa of all five species is attached to the substrate by a fine silk girdle around the thorax, and by a well-developed cremaster. There is no cocoon. The temporal cleavage line appears to be absent, although there is a very slight indication of a line running transversely across the top of the head. In each case (except for *heliconiaria* where a specimen was stored in alcohol) the pupa was attached to a leaf. However, as far as I know, pupation occurred in captivity in all specimens available so whether or not hedylid pupae are always attached to leaves in the wild requires confirmation.

Host-plant

Known only for *heliconiaria*: *Buettneria aculiata* Jacq., (Sterculiaceae). Recorded by Kendall (1976).

Habits

The following comments, on *heliconiaria*, are based on Kendall (1976), who has provided what appears to be the only published information. The eggs are laid singly on top of leaves of *Buettneria aculiata*. The larva eats a series of small holes in the leaf. At rest it lies along the midrib. Kendall notes that the adults of *heliconiaria* are diurnal, as opposed to nocturnal, which may be exceptional for hedylics. Similar observations were made for the larva of *cascaria* collected by T. Fox from Costa Rica (pers. comm.). The specimen was found lying along the midrib on the upper surface of the leaf. The leaf of the food-plant (unidentified) to which the pupal exuviae is attached is largely consumed. From what remains it is clear that the larva had eaten several holes in the leaf.

Parasites

Mirax sp. and *Apanteles* sp. (Braconidae), identified by P. M. Marsh, USDA, Washington D.C., have been reared from *heliconiaria* larvae (R. O. Kendall, pers. comm.).

Distribution

Found in Central and South America: recorded from Paraguay, Brazil, Bolivia, Peru, Ecuador, Colombia, Venezuela, Guyana, Surinam, French Guiana, Panama, Costa Rica, Honduras, Guatemala, British Honduras, Mexico, Cuba, and Trinidad.

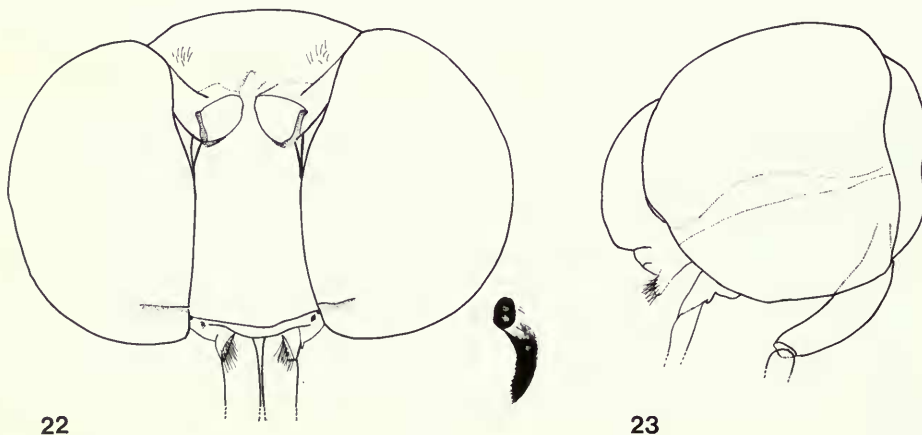
Specimens have been collected mostly from montane rain forest, occurring in many localities in the Andes. Material has been collected at localities up to 7000 ft.

Comments on selected structures

Adult

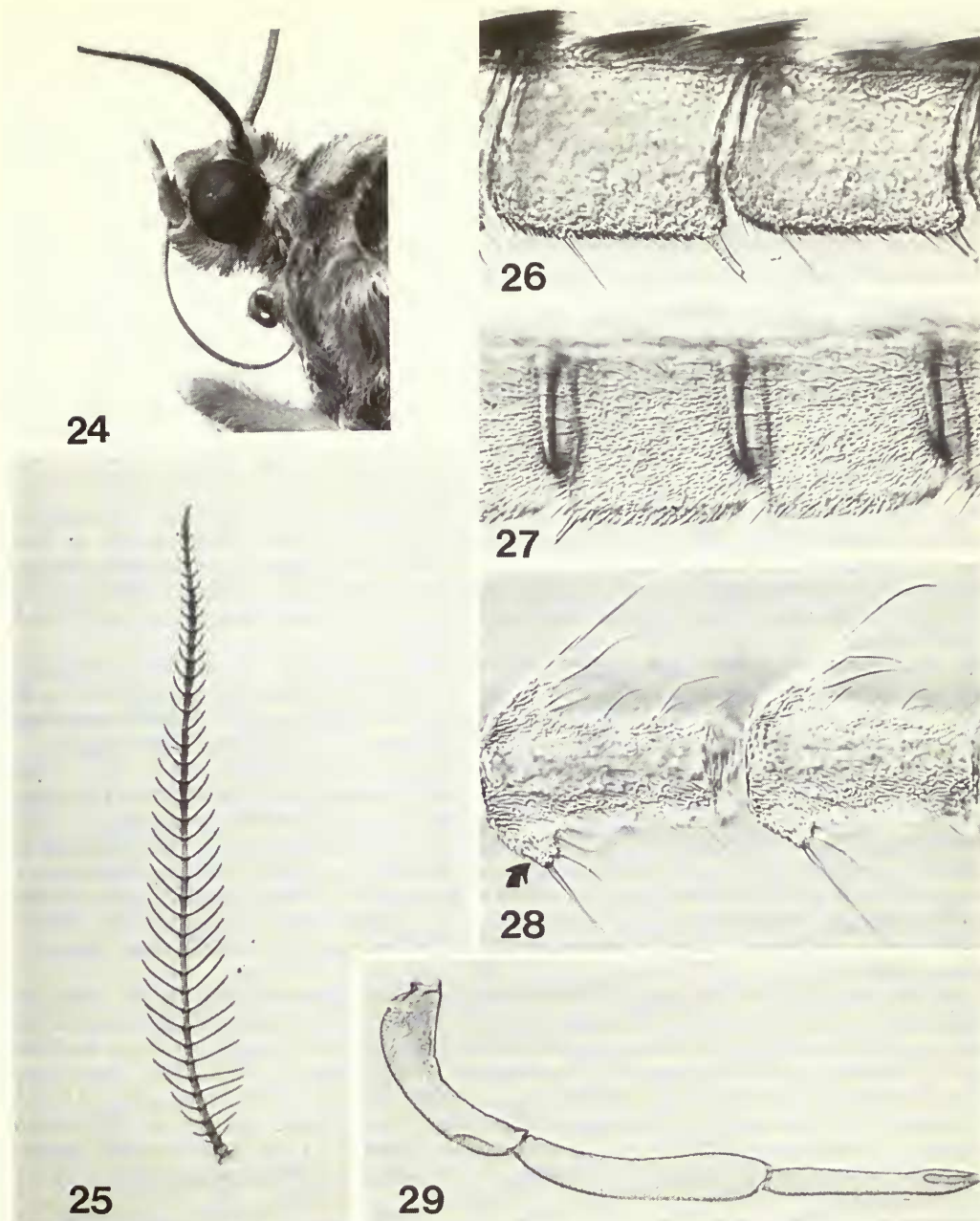
In this section further detail is provided about structures selected for their biological or systematic interest. Emphasis has been placed on comparing the Hedyliidae with other macrolepidopterans, and in particular the Rhopalocera. I include as macrolepidopterans the following taxa: Castnioidea, Hesperioidea, Papilionoidea, Geometroidea (sensu Common, 1970), Calliduloidea, Bombycoidea (including Sphingidae and Saturniidae), and Noctuoidea. (Geometroidea is used as a term of convenience in this work. Minet (1983) argued that the superfamily is not monophyletic.)

Head. The compound eyes are large and constitute a relatively large portion of the total area of the head (Figs 22–24). There is some variation in size between species. The inner, dorsal angle of each eye is weakly emarginate where it meets the base of the antenna (Fig. 22). Eye-size is of little value in assessing phylogenetic relationships of higher taxa since it is related to habits. Large eyes tend to be associated with low light intensity. However, the large eyes of most true butterflies, a group that is typically diurnal, 'are specialized for high visual acuity at the expense of relatively poor absolute sensitivity'. The reverse is apparently true of moths (Bernard, quoted in Ferguson, 1985). Most hedyliids are apparently nocturnal; on independent occasions, specimens have been collected at light by A. Watson, M. J. Matthews, and V. O. Becker (pers. comm.), and by the late C. L. Collette (label data). However, *heliconiaria* is said to be diurnal by Kendall (1976).



Figs 22, 23 Head of *Macrosoma tipulata* Hübner. 22, anterior aspect; 23, lateral aspect.

The narrow frons bulges moderately (Fig. 23), but not to the degree found for example in the Heliiothinae (Noctuidae). The narrowness of the frons means that the bases of the antennae are close together (Fig. 22). The antennae are usually filiform (Figs 26, 27), but in some species they are bipectinate (Fig. 25). In those with filiform antennae, the flagellar segments are rectangular, sometimes almost square, and each bears various sensilla. Usually the sensilla are long and arranged approximately in the shape of a 'U' on each side of the segments. They are shorter in females. In *tipulata* the segments are uniformly covered with shorter sensilla (Fig. 27). The more distal flagellar segments bear two or three longer setae, and also a sensillum basiconicum.



Figs 24–29 Head and associated structures of Hedyliidae. 24, head, lateral aspect, of *Macrosoma hyacinthina* (Warren), $\times 7.4$; 25, antenna of *M. semiermis* (Prout), σ ; 26–28, antennal segments of (26) *M. hyacinthina* (Warren); (27) *M. tipulata* Hübner; (28) *M. venodes* (Guenée), f , arrow indicates reduced pectination; (29) labial palpus of *M. tipulata* Hübner.

Bipectinate antennae are found in both sexes of *Macrosoma* (= *Hedyle*) *heliconiaria*, and its close relatives *M. semiermis* (Prout) (**comb. n.**), *M. inermis* (Prout) (**comb. n.**), and *M. albipannosa* (Prout) (**comb. n.**), and in males of *Macrosoma* (= *Venodes*) *napiaria* (**comb. n.**). In the females of *napiaria* each pectination is reduced to a small knob on each side of every flagellar segment (Fig. 28). In those species with bipectinate antennae each pectination bears sensilla. The sensilla in males are slightly longer than in females.

The antennae extend about one-half to just under two-thirds of the length of the fore wing. Whether filiform or bipectinate they bear lamellar scales dorsally.

Chaetosemata are present, one chaetosema behind each eye (Fig. 22). They are fairly small, but can be seen on dried specimens. Ocelli are absent. The presence of chaetosemata and the absence of ocelli are conditions found in Hesperioidea, Papilionoidea, and in many Geometroidea amongst macrolepidopterans. Chaetosemata are absent from the front of the head. According to Jordan (1923), most Hesperidae have a pair of chaetosemata additional to those on the vertex, sited between the crest of scales on the frons and the antennae. This additional pair is absent from papilionoids.

Mouthparts. The maxillary palpi are minute (Figs 22, 23), a condition found generally in larger lepidopterans. The proboscis is well developed. Its base is not scaled, which contrasts with the typically scaled condition found in Pyralidae. The labial palpus (Fig. 29) is three-segmented. The palpi are generally moderately ascending (Fig. 24) as a result of curvature of the basal segment, but are not appressed to the head as they are in papilionids and pierids. The invaginated sensory pit of the terminal segment is a character of the lepidopteran ground plan (Kristensen, 1984b). In those hedyliids examined for this character, the pit is deep, or moderately deep, and narrow.

Vestiture. Long narrow scales form the main covering of the frons and vertex (Fig. 24). These scales are neither closely appressed to the head, nor do they form a strongly erect tuft. The labial palpi are covered with scales; on the lower surfaces, particularly of the two proximal segments, they are long and narrow, forming a fringe (Fig. 24).

Thorax. To judge from the distribution of the sclerotized and membranous conditions of the patagia in true butterflies (Ehrlich, 1958b), the membranous condition must have arisen independently on several occasions. The sclerotized state is regarded as primitive. The development of membranous patagia has probably occurred independently in other macrolepidopterans, although the general condition (including that of hesperiids) is of sclerotized patagia. The loss of sclerotized patagia is given as a butterfly 'trend' by Ehrlich (1958b).

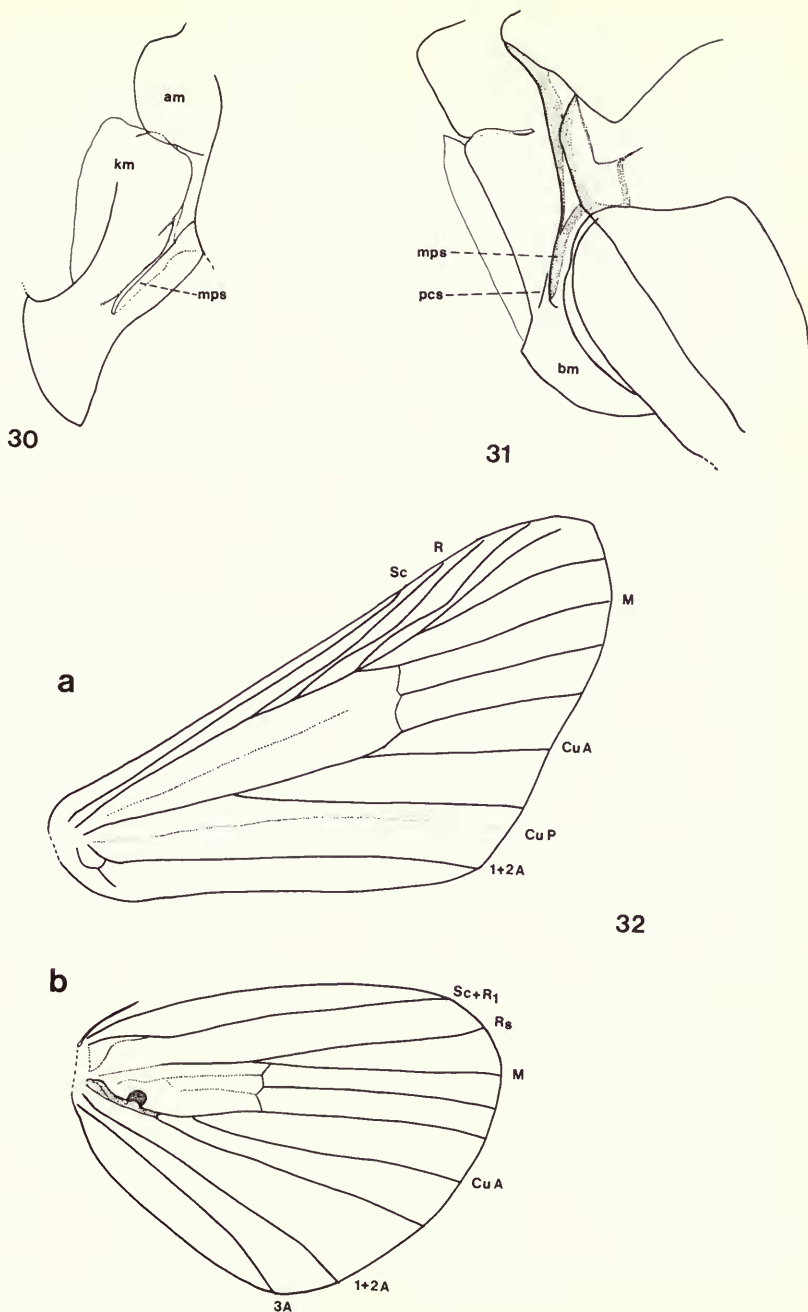
The size of the anepisternum of the mesothorax (Fig. 30) is not reduced, i.e., there is no pronounced dorsal movement of the anapleural cleft. A reduction is a prominent and specialized feature of Papilionoidea (Brock, 1971; figures of Ehrlich, 1958b). In Hesperidae the reduction is not so pronounced. Scott (1985) states that it is very large in moths and skippers; however, it is not large in all skippers.

In the mesothorax, the precoxal sulcus of hedyliids appears to be fused with the sulcus (Fig. 31) called 'marginopleural' by Shepard (1930) and Brock (1971). Usually these sulci are separate in the Lepidoptera. The precoxal sulcus does not curve towards the midline as it does in moths and skippers, and the basisternum is 'open' – not 'closed' by the sulcus. Brock (1971) drew attention to the divergent fused condition in papilionoids and noted that the primitive arrangement was retained in some Hesperidae, but almost reached the specialized condition in advanced members of the group. Scott (1985) observed that in hesperiids, although the precoxal sulcus (his paracoxal sulcus) might meet the 'marginopleural', it does not fuse with it as in papilionoids. These structures are difficult to interpret and need a broader survey to test their soundness.

There are two characters of particular importance in the metathoracic furca. In his study of the integumental anatomy of the Monarch butterfly, *Danaus plexippus* (L.), Ehrlich (1958a) noted that viewed dorsally the apophyses of the furca were shaped like an arrowhead. That this sagittate shape might be the general condition of both Hesperioidea and Papilionoidea was suggested by Brock (1971). (Brock treated the Hesperidae as a family of the Papilionoidea.) In the Hedyliidae the arrowhead is blunt, but nevertheless it is similar to that of other butterflies. The sagittate shape was not seen in the various macrolepidopterans examined by Brock. The shape is quite different in *Oenochroma vinaria* Guenée and *O. polypilla* Lower (Geometridae), and *Josia fornax* Druce (Dioptidae), which were examined during the course of this work.

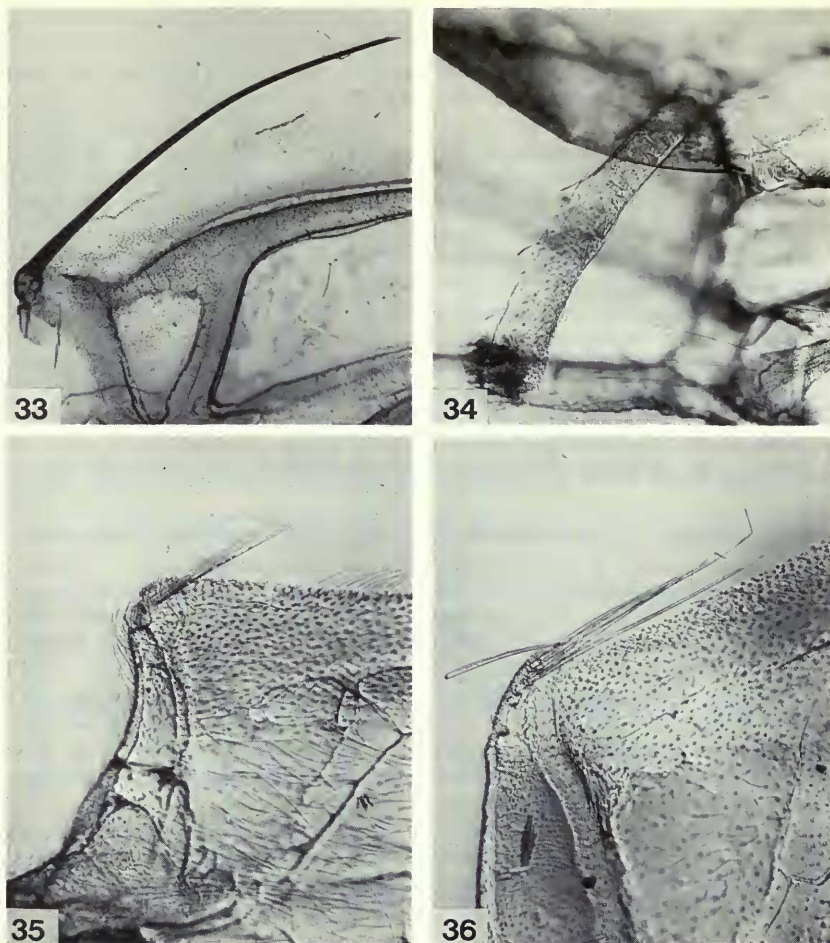
The character of the metathoracic furca considered by Brock (1971) to be the most prominent and divergent for the butterflies was that which he referred to as 'the peculiar mesal fusion of the dorsal laminae of the secondary arms from the point of their association with the apophyses to a point level with the thoraco-abdominal conjunctival insertion'. This character was also included as one of the shared derived (apomorphic) features of the Hesperioidea and Papilionoidea by Kristensen (1976). If I understand Brock's description correctly, this mesal fusion is present in the Hedyliidae. It can best be seen in dorsal view. Despite the weight given to this character by Brock (1971), the structure seems to be present in *Oenochroma vinaria* (Geometridae: Oenochrominae) and also in *Archiearis* Hübner, a member of the primitive geometrid subfamily Archiearinae.

Wing venation (Fig. 32a). The venation does not seem to vary between species either in the number of veins present, or their branching pattern and disposition. In the fore wing the arrangement of the veins of the radial sector (Rs) is characteristic of the family. The sinuous course run by Rs_1 and Rs_2 is such that they



Figs 30–32 Hedylidae. 30, 31, mesothorax of *Macrosoma rubedinaria* (Walker): (30) ventrolateral aspect, (31) lateral aspect; 32, *M. nigrimacula* (Warren) (a) fore wing, (b) hind wing; anepisternum (am), katapisternum (km), basisternum (bm), precoxal sulcus (pcs), 'marginopleural' sulcus (mps).

nearly meet at one point. The only stalking that occurs is that formed by the common stem of Rs_3 and Rs_4 . Veins R_1 , Rs_1 , and Rs_2 are all separate (at least from the cell). These veins fail to coalesce at any point so, unlike many macrolepidopterans, no secondary cells are formed. This pattern is generalized, and approximates to that exhibited by the more primitive of the macrolepidopteran elements. Unlike several lineages of higher Lepidoptera, there is no inward migration ('splitting back') of veins. The arrangement of



Figs 33–36 Wing-coupling apparatus in Hedyliidae. 33, frenulum of *Macrosoma hyacinthina* (Warren); 34, retinaculum of *M. bahiata* (Felder), view from ventral surface; 35, 36, frenular bristles of (35) *M. napiaria* (Guenée), ♂, (36) *M. satellitiata satellitiata* (Guenée), ♀.

Rs therefore provides few clues to relationships, although it further supports the exclusion of the group from advanced geometroids, calliduloids, bombycoids, and noctuoids.

Vein M_1 is remote from Rs_4 , a condition widely encountered, unlike the arrangement found in Epiplemidæ and Uraniidæ where these branches are associated. The usual geometroid condition, and indeed that of most higher Ditrysiæ, is that Rs_3 and Rs_2 share a common stem, and Rs_4 arises from this joint stem nearer to the cell (i.e. proximally). A notable exception is the Papilionoidea where Rs_3 and Rs_4 are often associated as in hedyliids. In the Hesperioidea there is no 'stalking' of the veins whatsoever; all run independently from the cell to the apex of the termen. Vein M is very weakly, but definitely, visible in the cell.

CuP is often present, but weak.

Hind wing venation (Fig. 32b). Vein $Sc+R_1$ is remote from Rs from the base of the cell; the condition contrasts with that found in geometrids and drepanids, but is not dissimilar from Epiplemidæ and Uraniidæ. The presence of two anal veins in the hind wing is more frequently encountered in the butterflies (including Hesperiidæ), bombycoids and noctuoids amongst the higher Ditrysiæ, than in geometroids (s.l.). The rather generalized occurrence of both these attributes therefore is of little value in assessing the relationships of *Macrosoma*. Nevertheless both features indicate yet further the remoteness of the genus from the Geometridæ.

M_2 does not arise nearer M_1 than M_3 .

Wing coupling (Figs 33–37). In males, a single-spined frenulum is usually well developed on the hind

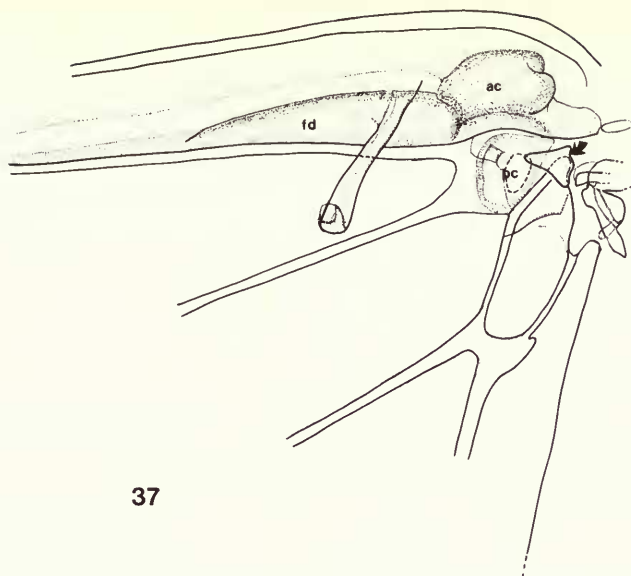


Fig. 37 *Macrosoma hyacinthina* (Warren), base of fore wing, ventral aspect; anterior chamber (ac), posterior chamber (pc), subcostal fold (fd).

wing (Fig. 33). It engages a long retinaculum on the fore wing (Figs 34, 37, 39). The length of the retinaculum is related to the need for it to extend over the prominent subcostal fold so as to engage the frenulum (Figs 37, 39). The frenulo-retinacular system is reduced and probably non-functional in the males of three species: *M. subornata* (Warren) (**comb. n.**), *M. leucoplethes* (Prout) (**comb. n.**), and *napiaria*. In the first two species the frenulum remains as a single spine, but it is much weaker and shorter. In *napiaria* it is reduced to a few short bristles (Fig. 35). The retinaculum of *napiaria* is lost, while in *subornata* and *leucoplethes* it is reduced to a very short, and presumably functionless structure. Although the frenulum and retinaculum are reduced in *subornata* and *leucoplethes*, the system is well developed in the closely related *M. desueta* (Prout) (**comb. n.**).

In females there are sometimes a few weak costal bristles on the hindwing (Fig. 36). There is no sign of a retinaculum, and functionally the frenulo-retinacular system is lost in this sex.

In Hesperioidea and Papilionoidea the frenulum and retinaculum are lost but remarkably, these structures are present in males of the hesperiid *Euschemon*. Scott (1985) notes that *Euschemon* is otherwise a typical pyrgine hesperiid and suggests an independent development of the frenulum and retinaculum through perhaps a reverse mutation. The loss of the frenulum and retinaculum or even of the retinaculum alone has occurred many times within the Lepidoptera besides the butterflies, e.g. in bombycoids, uraniids and some drepanids.

Wing surface. There is no holding area (*Haftfeld*) on the underside of the base of the fore wing and the metascutum of the thorax. These patches of velcro-like microtrichia (aculei) are absent from Hesperioidea, Papilionoidea, Geometroidea, and most Bombycoidea, a feature considered to be related to the resting position of the wings (Common, 1969; Kuijten, 1974). In general, those Lepidoptera with wings folded over the body have holding areas on the fore wings and thorax, whereas those with wings held vertically at rest or at right angles to the body do not.

Vestiture. Two kinds of scales predominate on the wing-surface (Fig. 38): (a) broad, 'typical', overlapping scales, and (b) hair-like scales. The wings appear to be hairy in parts. The broad scales do not provide a dense cover to the wings; hedyliids are relatively weakly scaled. In several species there are small hyaline patches devoid of scales, or larger areas with semi-transparent scales. The small hyaline patches may be seen with the naked eye on some specimens (Figs 10, 16). The hair-like scales are more dense on the basal section of the upperside, and somewhat more dense on the underside.

Figs 1–18 illustrates the main kinds of wing patterns in the Hedyliidae. Of particular note is that the markings on both dorsal and ventral surfaces are, with very minor exceptions, the same, compare Fig. 12 with Fig. 18. At least one hedylid may hold its wings vertically at rest so exposing the underside (R. O. Kendall, pers. comm.) although this requires confirmation. Such a resting position may be related to the strong patterning on the underside. In *M. subornata* the posterior half of the underside is pale and contrasts

sharply with both the rest of the underside and with that of the upper surface. The habit of holding the wings vertically is common among butterflies, and is also to be seen in several geometrids. (I am grateful to Dr K. Sattler for suggesting the resting position of hedyliids.)

There are several relatively distinct wing-patterns in hedyliids, as well as other patterns that are less distinct. Frequently, elements of one subgroup are found in another. For example, large areas covered by semi-transparent scales are present in many species as are small, but distinctive, white triangular marks on the costa of the fore wing near the apex. In some species the apex of the fore wing bears a large patch of either chestnut or dark brown. The illustrations show the distinctive emargination of the apex of the forewing, a condition found in many species, and the weakly falcate shape of them all. The comments that follow are an adjunct to the black and white photographs to provide a guide to colour.

M. heliconiaria (Guenée) (Fig. 1). Ground colour darkish grey-brown with translucent patches on fore and hind wings. The small triangular mark on the costa of the fore wing is white.

M. hyacinthina (Warren) (**comb. n.**) (Fig. 2). Ground colour dark grey-brown with a purple iridescence. More brown than grey at apex of fore wing. The pale patches on both wings are covered with semi-transparent scales except for the subtriangular mark on the costa of the fore wing, which is white.

M. tipulata Hübner (Fig. 3). A pale species. The wings bear large areas of semi-transparent scales. The darker areas are pale brown, and the small irregular patches on the fore wing are white, edged with darker brown.

M. rubedinaria (Walker) (**comb. n.**) (Fig. 4). Ground colour brown. The small dark streaks are dark brown, edged with white.

M. ustrinaria (Herrich-Schäffer) (**comb. n.**) (Fig. 5). A pale species. The darker scales scattered unevenly over the wing surfaces are pale brown.

M. leucophasiata (Thierry-Mieg) (**comb. n.**) (Fig. 6). The pale areas are white and the dark parts dark to very dark grey-brown.

M. subornata (Warren) (Fig. 7). Ground colour brown, dark brown near apices of wings. The patch on the costa is cream, and the patch below it and the tiny spot to one side are white. On the underside the posterior half of the fore wing is pale, contrasting markedly with the equivalent section of the upper surface.

M. paularia (Schaus) (**comb. n.**) (Fig. 8). Ground colour of fore wing pale grey-brown flecked and streaked with dark brown. The large spot at the apex of the fore wing is a warm pale brown. The large pale area on the hind wing is composed of semi-transparent scales.

M. coscoja (Dognin) (**comb. n.**) (Fig. 9). Ground colour pale brown. Apex of fore wing dark brown. The small patch at the base of the strong apical patch is composed of semi-transparent scales.

M. satellitiata (Guenée) (**comb. n.**) (Fig. 10). Ground colour a darker brown than that of *coscoja*. Otherwise similar to that species. The small 'white' spot at the base of the hind wing represents the glassy modification in males discussed below.

M. albifascia albifascia (Warren) (**comb. n.**) (Fig. 11). Ground colour grey-brown. The pale area on the fore wing is semi-transparent. The apex of the fore wing is a warm pale brown thickly edged with dark brown. The very dark streak and patches on the fore wing are also dark brown.

M. hedyllaria (Warren) (**comb. n.**) (Figs 12, 18). The colour pattern is extremely similar to *heliconiaria*, although the apex of the fore wing is more brown than grey-brown. The name *hedyllaria* is obviously a composite of *Hedyle* (the genus in which *heliconiaria* was described but which is treated as a junior synonym of *Macrosoma* in the present work) and *heliconiaria*.

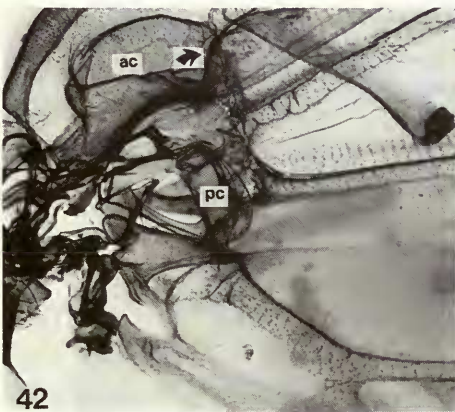
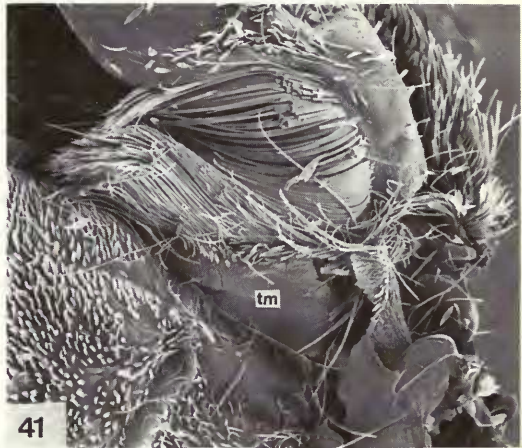
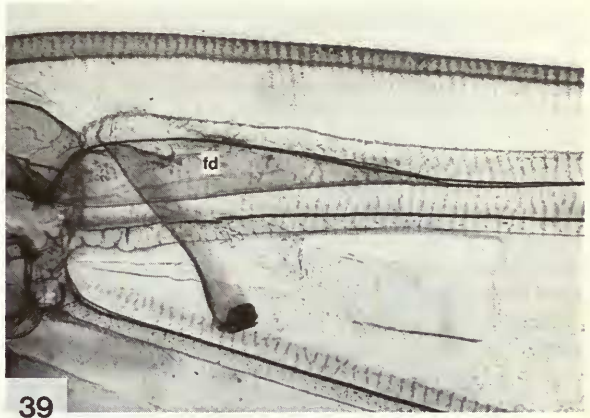
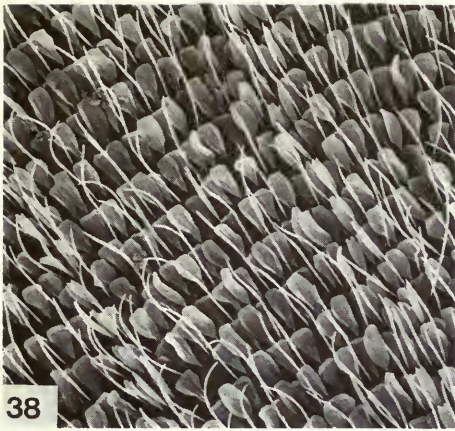
M. lucivittata (Walker) ♂ (Fig. 13). Ground colour brown. The pale areas are covered with semi-transparent scales and many brown piliform scales. ♀ (Fig. 14). Similar to the male but with a distinct semi-transparent spot near the apex of the fore wing.

M. nigrimacula (Warren) (Fig. 15). Ground colour brown, flecked and spotted with dark brown. The semi-transparent areas are poorly defined on the upper surface in this species. On the underside of the fore wing the posterior half bears a large pale grey area that contrasts with the rest of the wing.

M. leptosiata (Felder) (**comb. n.**) (Fig. 16). Ground colour brown. Both fore and hind wing edged with darker brown distally, particularly on the fore wing.

M. napiaria (Guenée) (Fig. 17). Ground colour off-white, formed by a covering of semi-transparent scales. The veins of the fore wing are a more strongly pigmented shade of cream.

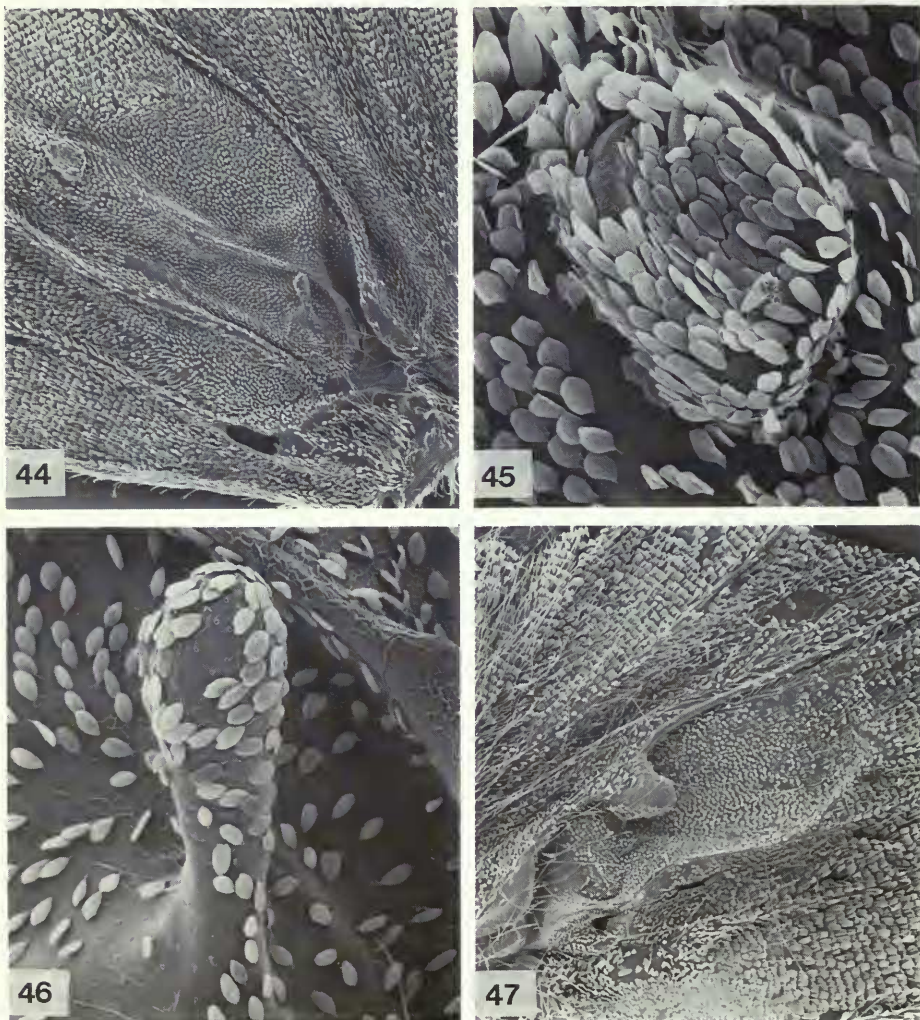
Modification of the fore wings (Figs 37, 39–43). The base of the fore wing bears some apparently unique modifications. These take the form of a ventral expansion of vein *Sc* into a fold, and the presence of two small, rounded chambers developed within the bases of certain veins. A pocket is also present and is enclosed by a dense fringe of scales. These modifications occur within both males and females. In addition, a distinct lobe is formed near the anal edge of the fore wing in males of some species.



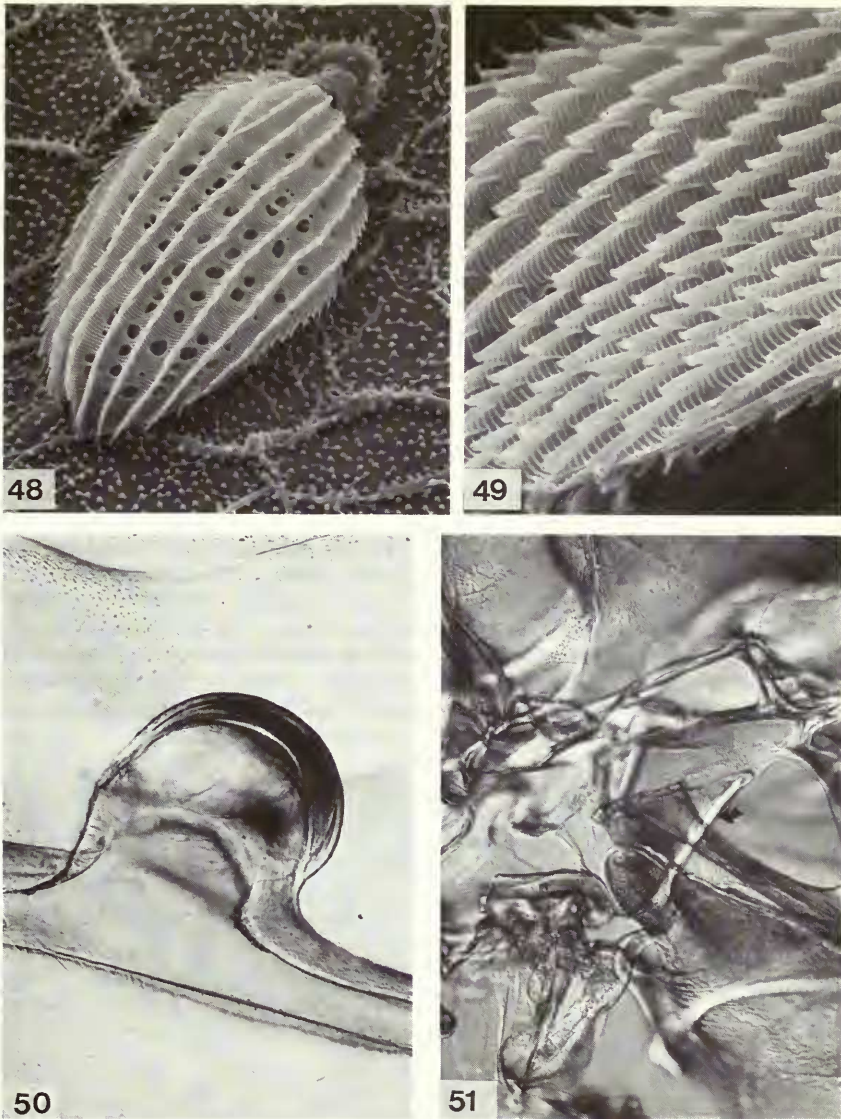
Figs 38–43 Fore wing structure (ventral aspects) of Hedyliidae. 38, vestiture of fore wing of *Macrosoma tipulata* Hübner; 39, base of fore wing of *M. hyacinthina* (Warren) to show subcostal fold (fd); 40, 41, scanning electron micrographs of base of fore wing of *M. tipulata* Hübner; (40) $\times 16$, large arrow indicates pocket, small arrow shows base of retinaculum, (41) detail of pocket $\times 40$, ? tympanum (tm); 42, base of fore wing of *M. hyacinthina* (Warren), arrow indicates position of membrane (see text); 43, lobe at base of fore wing of *M. hyacinthina* (Warren).

The expansion of *Sc* on the underside of the fore wing is prominent (Figs 37, 39, 40). There is some variation in its extent between species, but the form is basically similar. This fold is a hollow outgrowth of the vein (although both membranes are close together and not 'ballooned'). The fold extends a short way along the wing. At the extreme base of the fore wing, *Sc* is expanded into a hollow chamber (Figs 37, 42) the main part of which lies ventral to the plane of the wing. This chamber is divided from the fold by a membrane that runs at right angles to the plane of the wing. The position of this membrane is arrowed in Fig. 42; it is visible as a dark line in this view. The chamber is invaginated caudally providing another pocket, which is enclosed by a thick fringe of hair-scales (Figs 40, 41). The posterior wall of the chamber is invaginated. From the ventral exterior lip of this invagination arises a thick fringe of hair-scales (Fig. 40 and particularly Fig. 41). Below this fringe, and presumably protected by it, is an extremely delicate, transparent membrane. This is supported by a cuticular frame at the base of *Cu*, also lying in the ventral plane of the wing. Stretched over the other (posterior) side of this frame is a whitish membrane, which closely resembles the tympanum found in the auditory organs of certain Lepidoptera (Fig. 41).

Lying mainly within the dorsal plane of the fore wing is another small, closed chamber (Figs 37, 42). This chamber is an expansion of the base of the cubitus, '*Cu*₂' in the terminology of Sharplin (1963).



Figs 44–47 Scanning electron micrographs of specialized structures on hind wing (ventral aspects) of Hedylidae. 44–46, *Macrosoma tipulata* Hübner: (44) general view of area $\times 16$, (45) detail of squat protuberance, $\times 140$, (46) detail of finger-like protuberance, $\times 160$; 47, *M. zikani conifera* (Warren) (comb. n.), base of hind wing $\times 16$.



Figs 48–51 Wing structures of Hedyliidae. 48, 49, scale from specialized area of hind wing (ventral surface) of *Macrosoma tipulata* Hübner, (48) whole scale, $\times 2600$, (49) detail to show serrations $\times 6500$; 50, specialized structure near base of hind wing (ventral surface) of *M. nigrimacula* (Warren); 51, base of fore wing of *M. hyacinthina* (Warren) to show position of second median plate partly hidden under 1A (arrowed).

Although the function of these chambers is unknown, there are several similarities with the tympanal organs found at the base of the fore wing in many nymphalid butterflies. The structure of these alar tympanal organs is summarized by Bourgonne (1951). In both hedyliids and those nymphalids with these organs, the tympanum is situated at the base of vein *Cu*. Unlike thoracic or abdominal hearing organs, there is no tympanic cavity; instead, the tympanum is superficial. In nymphalids, the membrane is protected by scales, but in hedyliids it is more exposed. In most of those nymphalids with alar hearing organs, veins *Sc* and *Cu* are swollen basally, and the tracheal air sacs within the swellings communicate with the tympanic sac (Bourgonne, 1951). It is uncertain whether there is a functional relationship between the sacs, but it should be noted that not all nymphalids with hearing organs have swollen veins. In the Hedyliidae the veins are not swollen.

It is well known that some butterflies respond to sound. Swihart (1967) demonstrated the sensitivity to

sound of a small chamber at the base of each *hind wing* of *Heliconius erato* (L.). He also found a similar, but smaller, chamber at the base of each fore wing.

No information is available on the question of whether hedyliids respond to sound, but on circumstantial evidence it seems likely that the modifications at the base of the fore wing function as an auditory organ.

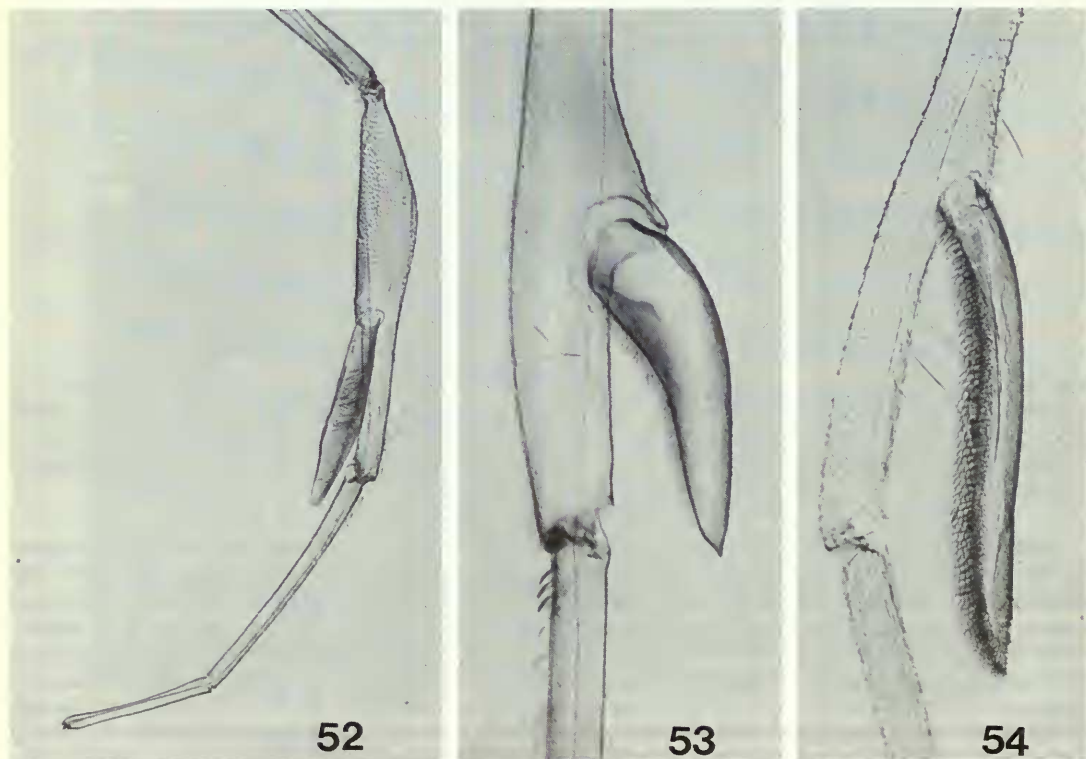
The possibility that the chamber enclosed by the fringe of hairs is a scent pouch cannot be discounted, but the pocket is present in both males and females. The presence of 'scent pockets' tends to be sexually dimorphic in lepidopterans, but is not always so.

A small lobe extends from the anal edge of the fore wing near its base in the males of some species. It is prominent in *hyacinthina* (Fig. 43). A very weakly developed expansion of this area is found in many species.

Modifications of the hind wing (males). These are present in many species. Viewed with the naked eye they appear as small, oval, glassy areas at the base of the wing on both the upper and the under sides (Figs 10, 16). The modifications take the form of a folding of the wing membrane, making the surface appear rather crinkled or distorted when viewed under a dissecting microscope. Their appearance under the scanning electron microscope is shown in Figs 44 and 47. From this area one or more protuberances arise on the under side of the wing (Figs 44–47, 50). The area is covered with specialized scales.

In *hyacinthina* the modified area may be roughly divided into an inner, approximately oval section, which bears short piliform scales on both surfaces, and an outer section with both piliform scales and semi-transparent laminar scales. A prominent knob-like structure is present on the underside.

The modifications of the hind wing are well developed in many other species, and less pronounced in several more. Modifications present in one species may be absent from closely related ones. In *M. bahiata* (Felder) (**comb. n.**) for example they are present, while in *coscoja*, a close relative, they are not. In the same group of species the structures are less strongly pronounced in *M. albistria* (Prout) (**comb. n.**) and *M. uniformis* (Warren). In *tipulata* two protuberances are present (Fig. 44) of which one is relatively squat (Fig. 45), and the other is a long digitate structure, which is slightly swollen apically (Fig. 46). The function of these protuberances is uncertain, but since they are confined to the males they are probably scent organs of some kind. Figs 48 and 49 illustrate the specialized scales found on the surface of the structure in *tipulata*. The longitudinal ridges are strongly serrated (Fig. 49).



Figs 52–54 Fore legs of male Hedyliidae. 52, *Macrosetia semiermis* (Prout), tibia and tarsus; 53, 54, epiphysis of (53) *M. tipulata* Hübner, (54) *M. napiaria* (Guenée).

Wing base. According to Dr R. de Jong (pers. comm. and in prep.), to whom I am indebted for sketches and information, the second median plate of the fore wing is always partly hidden under the base of vein 1A in both Hesperioidea and Papilionoidea. The general ditrysian condition seems to be that the plate is not obscured by 1A. In the Hedyliidae the second median plate is small and partly obscured by 1A (Fig. 51).

Legs. An epiphysis is present on the fore leg of both males and females (Figs 52–56). The presence of this structure is widespread among macrolepidopterans including the Hesperioidea (with a few exceptions) and Papilionidae, but it is lost in many Pieridae, Nymphalidae, Libytheidae, and Lycaenidae.

In males the fore tarsi are modified (Figs 55, 58). Although they are not reduced in length (in fact they are long or very long) the segments are mostly fused so that only a long proximal segment and a short distal segment are present. In *tipulata* the proximal segment is extremely long (Fig. 55).

The pretarsus of the fore leg is reduced to a pair of small claws in males (Figs 52, 58). In some species these claws are minute, and in all species they are only very weakly curved. There is no arolium, or empodium, nor are there pulvilli on the fore tarsi of males. The fore tarsi bear a prominent fringe of piliform scales giving them a feathery appearance. There are no spines.

In females the fore tarsi are not modified (e.g. *tipulata*, Fig. 56). There are five tarsomeres and the pretarsus bears claws that are strongly curved and asymmetrically forked, pulvilli, and a large arolium. The tarsomeres are covered with laminar, not piliform, scales, and a series of small spines is present.

The mid and hind tarsi in both males and females are five-segmented, spined, and with a normally developed pretarsus with claws, pulvilli and an arolium. The mid leg is generally longer than the hind leg, but shorter than the fore leg.

Microtrichia or aculei ('tiny spines' of Scott, 1985) are not present on the dorsal aspect of the tarsi, unlike the Papilionidae, Pieridae, some Nymphalidae and some Lycaenidae. According to Scott they are absent from hesperiids and from other macrolepidopterans. Microtrichia are, however, present on the ventral aspect of the tarsi of Hedyliidae although their distribution is patchy, being best developed on the pulvilli. They are absent from the fore tarsi of males. Ventral microtrichia are probably widespread in Lepidoptera.

A single pair of tibial spurs is present on the midleg of both sexes (Fig. 61). The hind leg of the male of *tipulata* bears two pairs of tibial spurs (Fig. 62), but usually hedyliids (including the female of *tipulata*) have one pair distally on the hind tibia. The proximal pair of spurs is found in many Lepidoptera, e.g. some Thyrididae, some Hesperioidea, some Drepanidae, many Bombycoidea (including Sphingidae), and many Noctuoidea (including Notodontidae). This loss is a classic example of a character that is prone to independent reduction in many groups. Therefore the loss of spurs in most hedyliids and in papilionoids does not provide strong evidence for their monophyly. In one female specimen of *hyacinthina* there is apparently no pretarsus at all on the hind leg: the tarsus ends in a flask-shaped tarsomere (Fig. 60). There is no sign of claws arising from this last tarsomere. Of the two other females in the collection of the British Museum (Natural History), one has lost both hind legs while in the other the tarsi, including the pretarsus, are normal. In many species the hind tibia is slightly swollen.

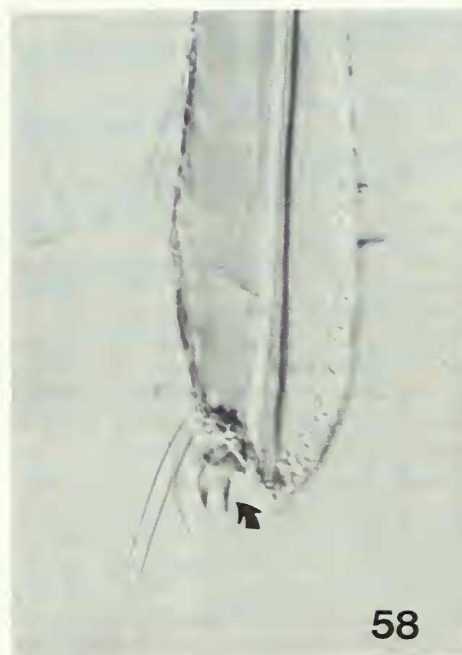
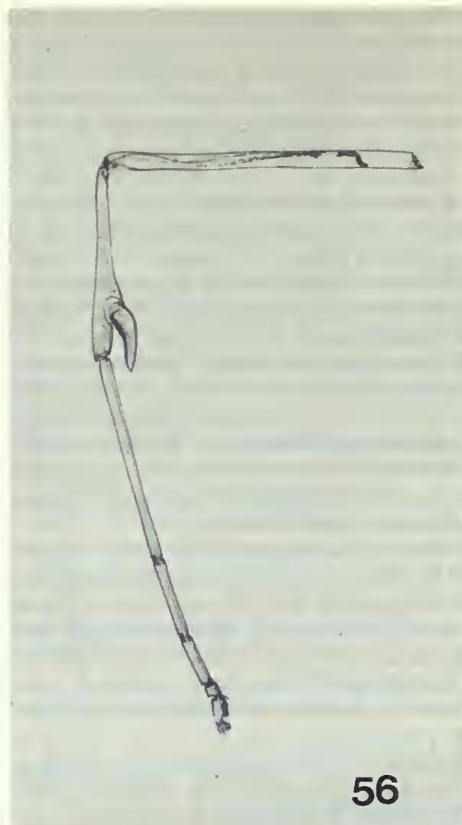
A scent pencil occurs on the fore tibia of males of five species (*hyacinthina*, *lucivittata*, *M. klagesi* (Prout) (comb. n.), and *nigrimacula*, and probably (only one specimen available) on *M. latiplex* (Dognin) (comb. n.)). The pencil comprises a bunch of long hairs arising from the inner surface of the tibia. It is particularly well developed in *hedyllaria*.

The modifications of the legs of the Hedyliidae are all found within other butterflies. Information for Hesperioidea and Papilionoidea is summarized in a useful table by Scott (1985: table 1). Pulvilli and the arolium are lost from the legs of Papilionidae, some Pieridae, and some Nymphalidae. In the Papilionidae and the Pieridae the tarsomeres are not fused. In Nymphalidae the male fore legs are small although the tarsomeres are not lost or fused. In Lycaenidae the male fore legs are reduced to a single tarsomere together with reduction or loss of claws. The proximal pair of tibial spurs on the hind leg is absent from all true butterflies (Ehrlich, 1958b; Scott, 1985) and hedyliids (with the exception of the male of *tipulata*), but these spurs are present in skippers. Scent brushes, when present, tend to be found on the hind legs of butterflies; they occur on the fore legs of Hedyliidae.

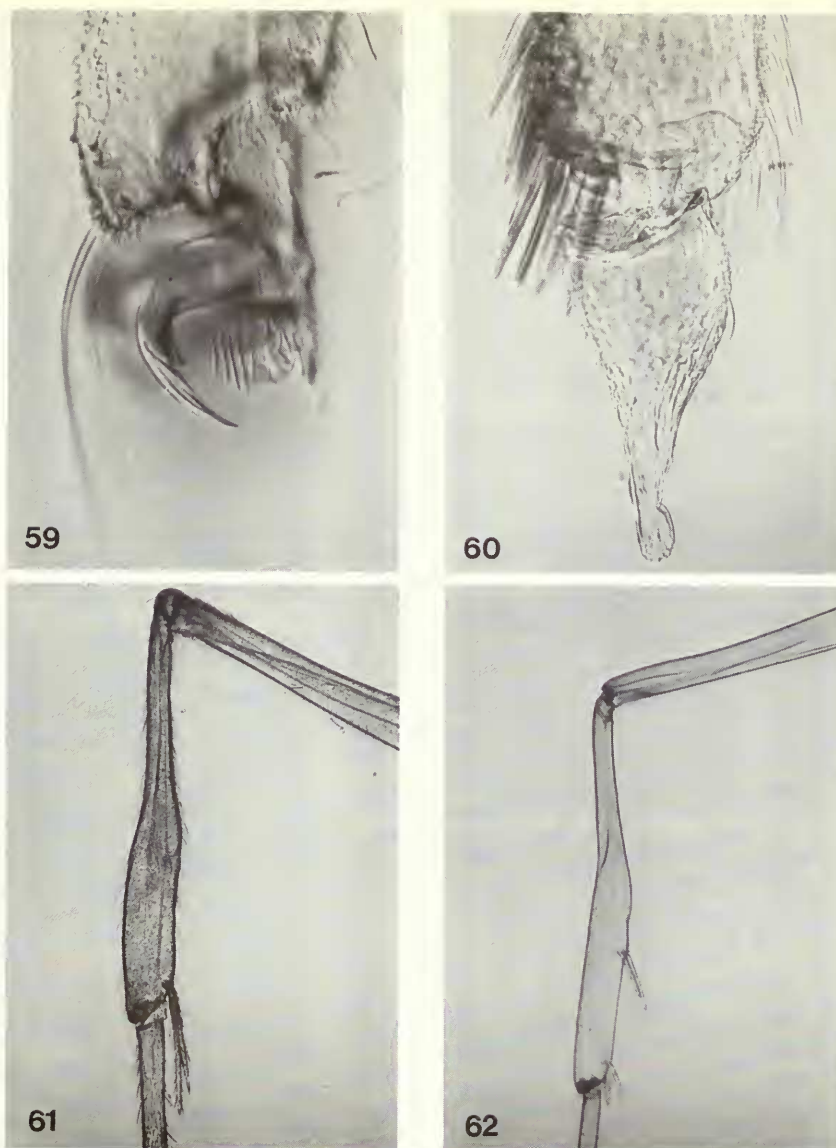
Abdomen. The abdomen is distinctly curved, particularly in males (Fig. 63), and is laterally flattened. Not only are these features butterfly-like, but from my initial observations they resemble true butterflies (Papilionoidea) rather than skippers (Hesperioidea). This interpretation, however, remains tentative.

Tergum I is 'pouched' (Figs 64, 68), that is, there is a pocket-like outgrowth of tergum I posteriorly that overlaps tergum II. Ehrlich (1958b) used the word 'pouched' to describe the typical papilionoid condition. The pouching in hesperioids is not strong, and in some papilionoids the pouch is reduced (Ehrlich, 1958b).

On segment I there are pre- and postspiracular bars. The prespiracular bar (Figs 64, 68) is a narrow sternopleural structure, which extends anteriorly from the antero-lateral margin of sternum II, and curves around the spiracle. The presence of a prespiracular bar is the general condition in macrolepidopterans, including hesperioids and papilionoids, although it is lost in pierids (Ehrlich, 1958b). The presence of this



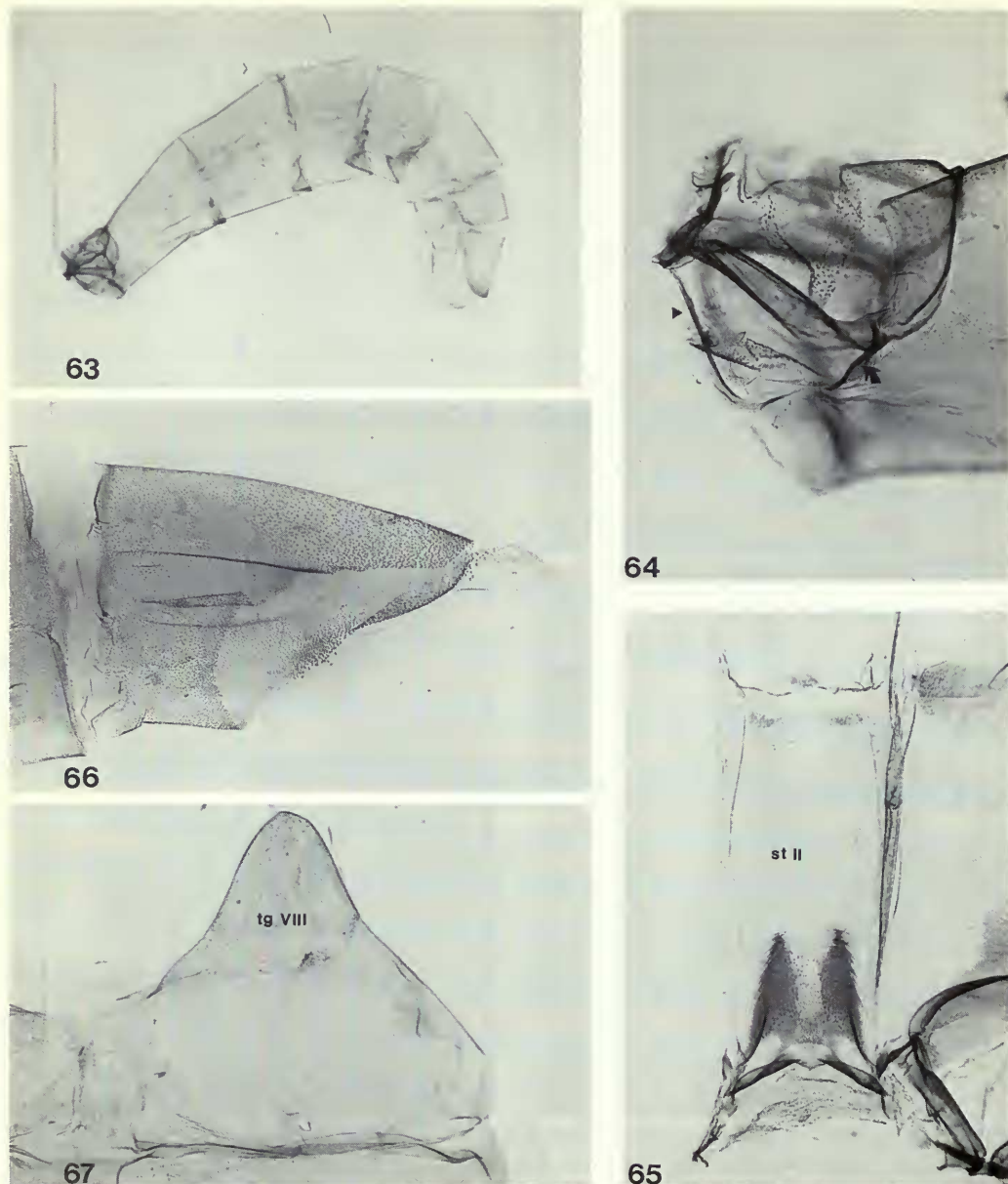
Figs 55–58 Fore legs of Hedylidae. 55, 56, *Macrosoma tipulata* Hübner: (55) ♂, (56) ♀; 57, *M. hedylaria* (Warren), ♂; 58, *M. semiermis* (Prout), tarsal claws of ♂, arrowed.



Figs 59–62 Legs of Hedyliidae. 59, pretarsus of *Macrosoma tipulata* Hübner, ♀, showing weak fork of claw; 60, last (5th) tarsal segment of hind leg of *M. hyacinthina* (Warren), ♀; 61, 62, hind tibia of (61) *M. hedyllaria* (Warren), ♂, (62) *M. tipulata* Hübner, ♂.

structure in the Hedyliidae is therefore of no particular phylogenetic significance. Brock (1971) considers that both pre- and postspiracular bars are secondarily developed within the Papilionoidea and Hesperioidea (his Papilionoidea) and analogous to similar structures in certain Pyraloidea, Geometroidea and Noctuoidea. It is not entirely clear why Brock does not consider them homologous.

The postspiracular bar is well-developed in the Hedyliidae. It is a tergopleural structure (Figs 64, 68), which just fails to meet the sternum. According to Brock (1971) the postspiracular bar is derived from terga I and II. Ehrlich (1958b) considered the presence of a postspiracular bar to be specialized within the Papilionoidea, where he presumably considers it to have evolved independently within the group. Scott (1985) records the bar as absent in Papilionidae (Ehrlich said it was reduced or absent), present or absent in Nymphalidae, present and large in Libytheidae, and absent in Lycaenidae. He notes its presence in or absence from Hesperioidea and its absence from other macrolepidopterans. Both Ehrlich and Scott consider the structure as derived. The occurrence of a similar structure in some other macrolepidopterans



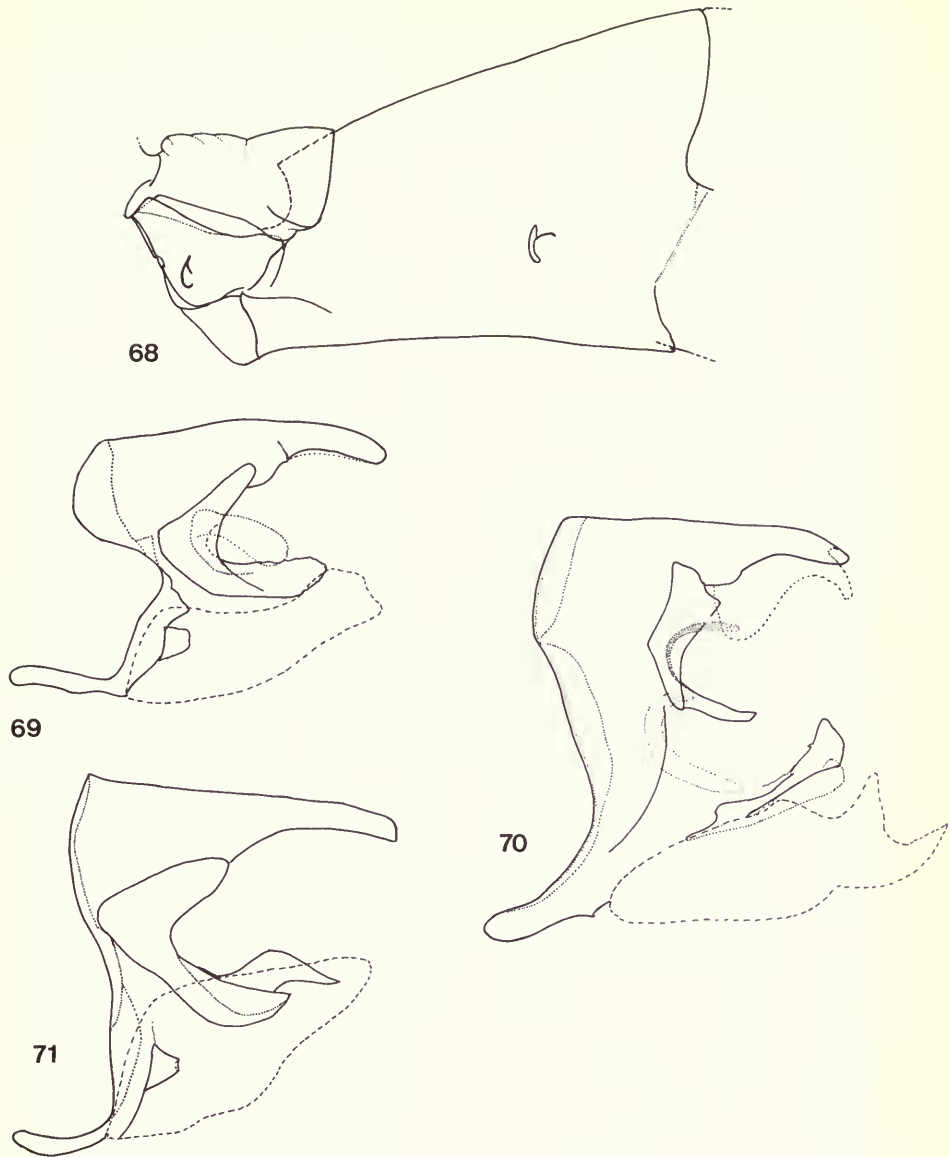
Figs 63–67 Abdomen of Hedyliidae. 63, 64, *Macrosoma bahiata* (Felder), lateral aspect: (63) whole abdomen, (64) base of abdomen, small arrow – pre spiracular sclerotization, large arrow – post spiracular sclerotization; 65, sternum II (st II) of *M. paularia* (Schaus); 66, segment VIII of *M. semiermis* (Prout), ♂, lateral aspect; 67, tergum VIII (tg VIII) of *M. tipulata* Hübner, ♂.

(e.g. Thyrididae) noted by Brock is probably too isolated to suggest that the structure in the butterflies is not derived.

The tergal groove is well developed and leads into a strong tergal brace – the internal ridge of the groove (Fig. 64).

There are no abdominal tympanal organs in the Hedyliidae.

Male genitalia (Figs 69–89). The lateral arms of the vinculum are long, so the genital capsule appears 'deep', that is, expanded dorso-ventrally. The natural way to mount these structures for microscopic slide preparation is laterally, since if they are mounted ventrally they tend to topple over on the slide. Most

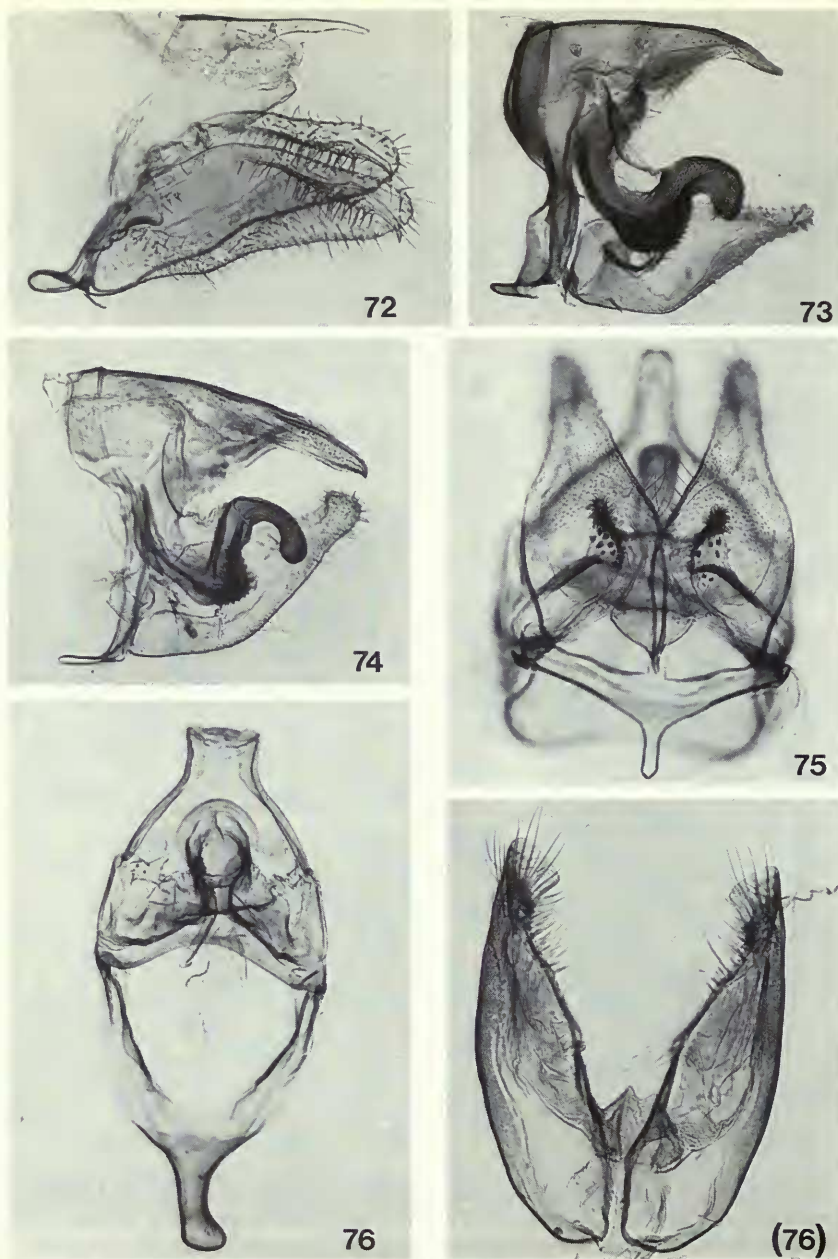


Figs 68–71 Abdomen and male genitalia of Hedylidae. 68, segments I and II of *Macrosoma bahiata* (Felder), lateral aspect, abbreviations as for Fig. 64; 69–71, male genitalia, lateral view, of (69) *M. semiermis* (Prout), (70) *M. hyacinthina* (Warren), (71) *M. paularia* (Schaus).

butterfly systematists mount male genitalia laterally for the same reason. The genitalia of the Hedylidae are similar to those of many butterflies in the shape of the genital capsule. They might be regarded as fairly generalized butterfly genitalia, but this does not provide strong evidence for the monophyly of hedyliids and other butterflies since the arrangement might be primitive. Certainly the Castniidae also have genitalia that are 'deep'. The lateral arms are fused with the tegumen so that segment IX of the abdomen forms a closed ring (e.g. Figs 73, 74), a feature noted as a tentative ground plan character of the Amphiesmenoptera (Kristensen & Nielsen, 1979: 126; Kristensen, 1984b: 150). The condition frequently encountered in the Lepidoptera is that of a distinct separation of the tergum and sternum of segment IX.

The valva is approximately triangular, and unmodified. This condition is found in many species of macrolepidopterans including many butterflies.

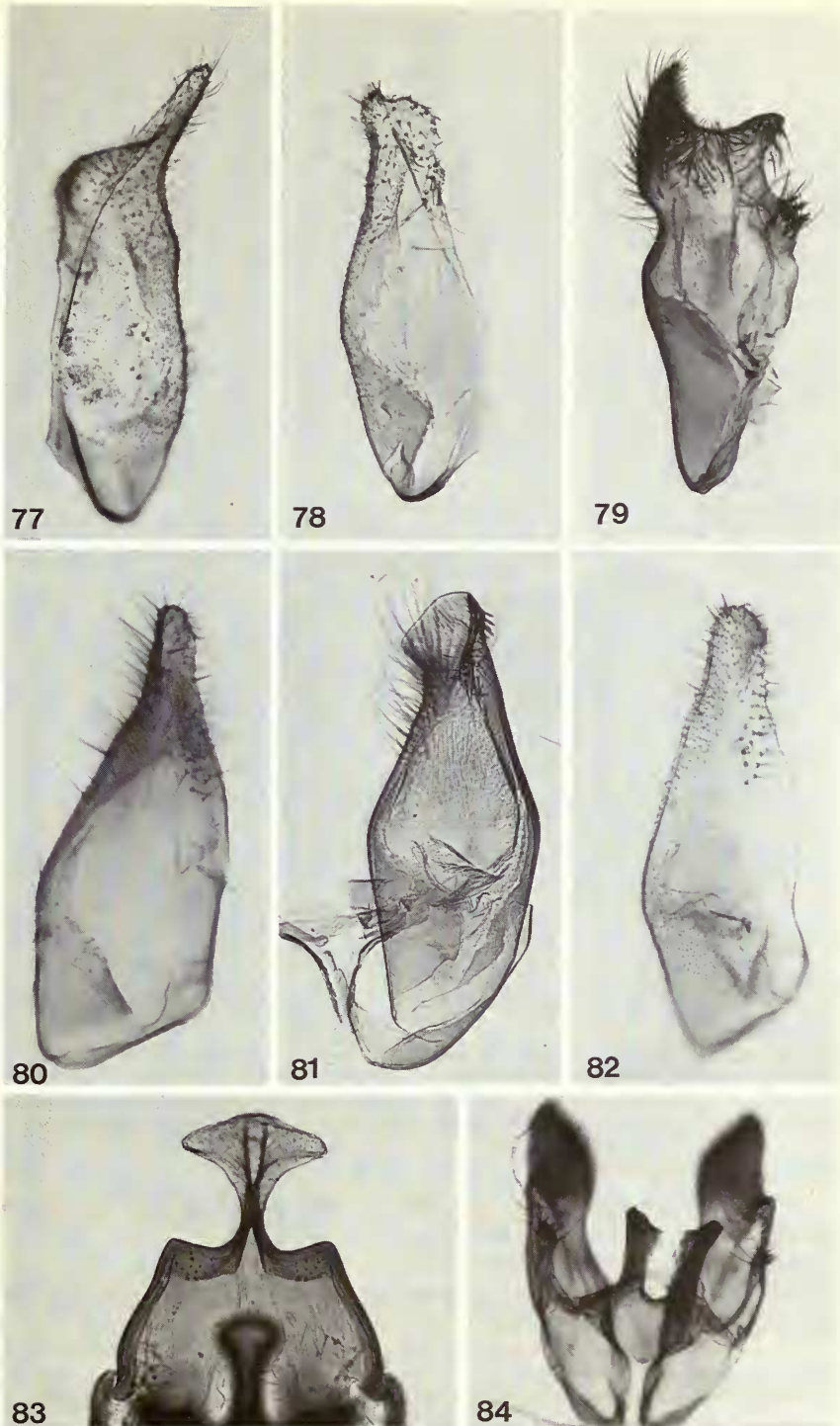
There are no particularly striking modifications of the main components of the genitalia. The greatest



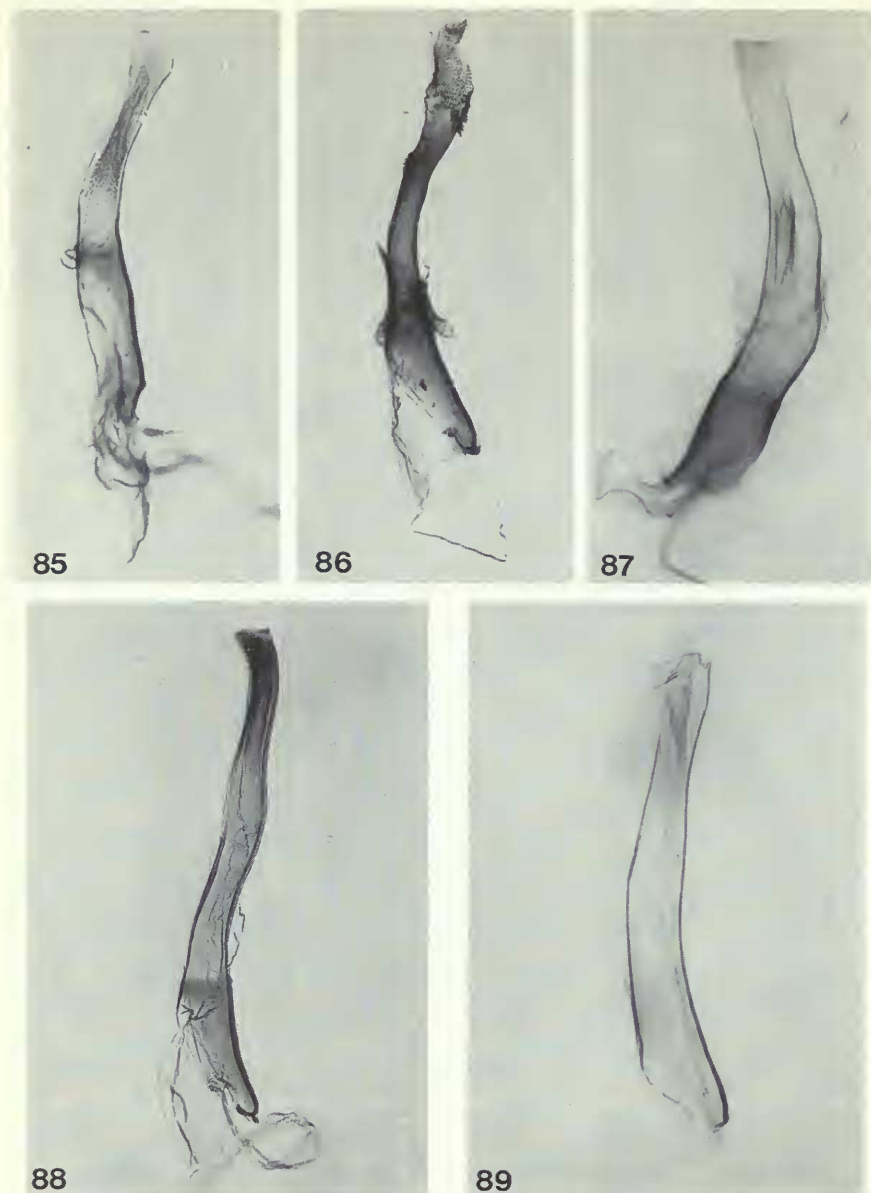
Figs 72–76 Male genital capsules of Hedyliidae. 72–74, lateral aspects of (72) *Macrosoma tipulata* Hübner, (73) *M. lamellifera* (Prout), (74) *M. napiaria* (Guenée); 75, 76, ventral aspects of (75) *M. napiaria* (Guenée); 76; *M. nigrimacula* (Warren) (a) valvae and juxta removed, (b) valvae and juxta.

modifications are the shapes of the uncus in *heliconiaria* (Fig. 83), the valva (Fig. 79) and juxta (Fig. 84) of *hyacinthina*, and the simplification of the genitalia of *tipulata* (Fig. 72).

Female postabdomen and genitalia (Figs 90–99). Tergum VII is longer than tergum VI and forms a weak hood over the genitalia, when they are not extended. Tergum VIII is well-sclerotized and narrow (Fig. 90), and gives rise to a pair of thin, anterior apophyses. In most species examined these are sclerotized, but in some they are membranous (staining in Chlorazol black E), and short (Figs 93, 96). Presumably, in those species with reduced apophyses the muscles are functionless during oviposition. In *hyacinthina* and



Figs 77–84 Male genitalia of Hedyliidae. 77–82, valvae of (77) *Macrosoma heliconiaria* (Guenée), (78) *M. semierris* (Prout), (79) *M. hyacinthina* (Warren), (80) *M. lamellifera* (Prout) (**comb. n.**), (81) *M. nigrimacula* (Warren), (82) *M. napiaria* (Guenée); 83, uncus of *M. heliconiaria* (Guenée), ventral view; 84, juxta of *M. hyacinthina* (Warren), valvae at different plane of focus.

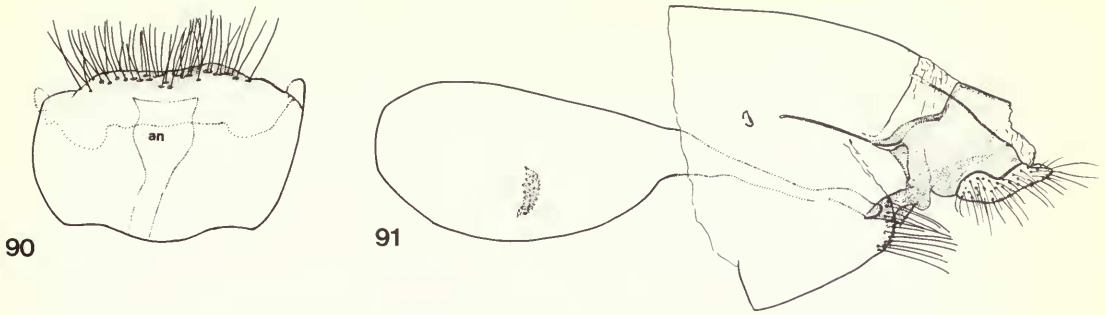


Figs 85–89 Male genitalia, aedeagus, of Hedylidae. 85, *Macrosoma heliconiaria* (Guenée); 86, *M. hyacinthina* (Warren); 89, *M. napiaria* (Guenée).

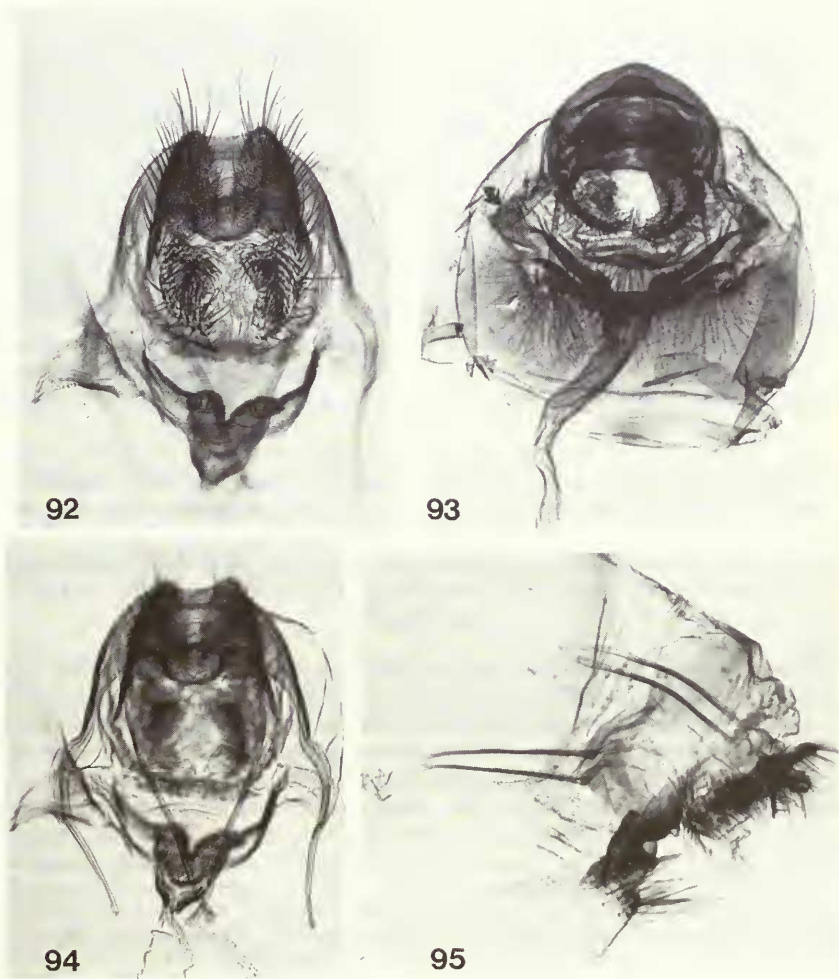
hedylaria the reduced anterior apophyses are usually bent inwards (medially) at their ends at about right angles. Reduced anterior apophyses are found in many butterflies.

Terga IX and X form a sclerotized band more narrow than tergum VIII. The posterior apophyses, which are derived from this, are sclerotized rods.

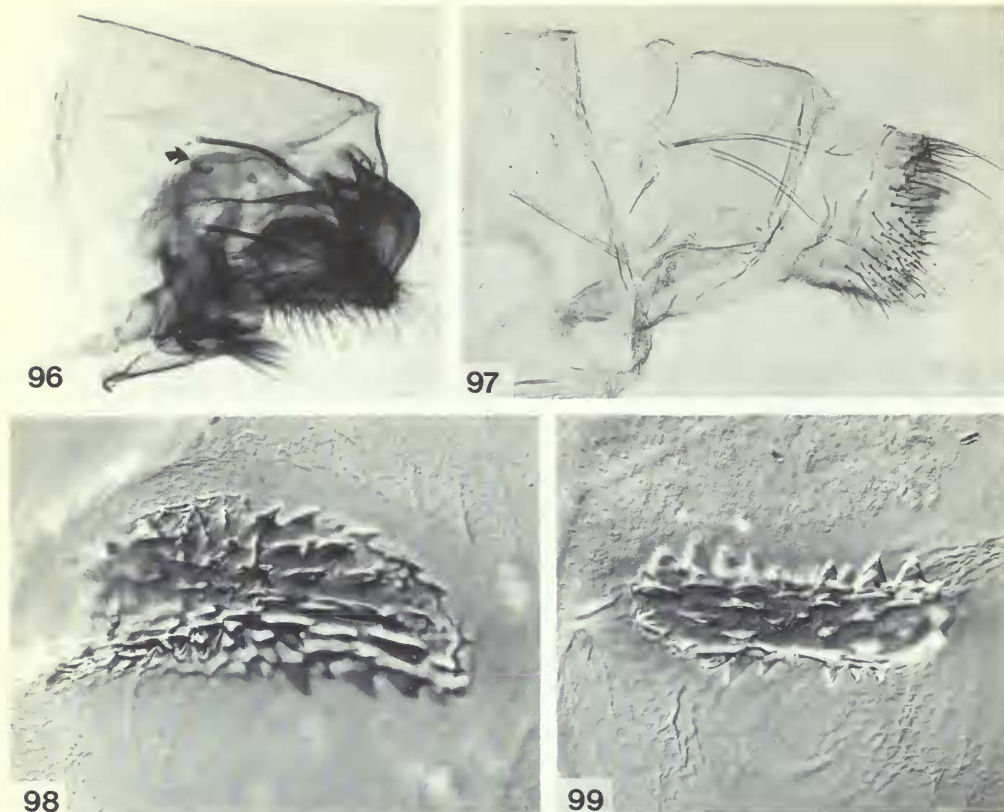
Ventrally, sternum VII is folded before the ostium bursae thus forming a lip to this aperture. The lip is nearly always fringed with strong setae (Fig. 90). The sclerotizations around the ostium bursae include anterior, posterior, and lateral components. The antevaginal and postvaginal sclerites are small, while the lateral sclerites (derived from sternum VIII) are large and extend laterally to unite with the anterior apophyses in those species where they are sclerotized. The extent of these ostial sclerotizations varies between species. In *heliconiaria* the lamella postvaginalis is absent as are the setae on the fold of sternum VII. In *tipulata* the sclerotizations are virtually absent (Fig. 97).



Figs 90–91 Female postabdomen and genitalia of Hedyliidae. 90, *Macrosoma hedyllaria* (Warren), abdominal sternum VII, ventral aspect, antrum (an); 91, *M. lucivittata* (Walker), lateral aspect.



Figs 92–95 Female genitalia of Hedyliidae. 92–94, ventral aspect of (92) *Macrosoma rubedinaria* (Walker), (93) *M. hyacinthina* (Warren), anterior apophysis arrowed, (94) *M. rubedinaria* (Walker) to show well-sclerotized anterior apophyses; 95, *M. lucivittata* (Walker), lateral aspect.



Figs 96–99 Female genitalia of Hedylidae. 96, 97, lateral aspect of (96) *Macrosoma hedylaria* (Warren), anterior apophysis arrowed, (97) *M. tipulata* Hübner; 98, 99, signum of (98) *M. lucivittata* (Walker), (99) *M. rubedinaria* (Walker).

The ostium bursae leads into the ductus bursae, the first part of which is funnel-shaped with sclerotized walls, the antrum (Fig. 94). Beyond this the ductus bursae is narrow, membranous, and usually long. It expands suddenly into a globose or slightly elongate-globose membranous corpus bursae (Fig. 91). The corpus bursae may bear a single signum of a characteristic shape (Figs 98, 99), or the signum may be absent.

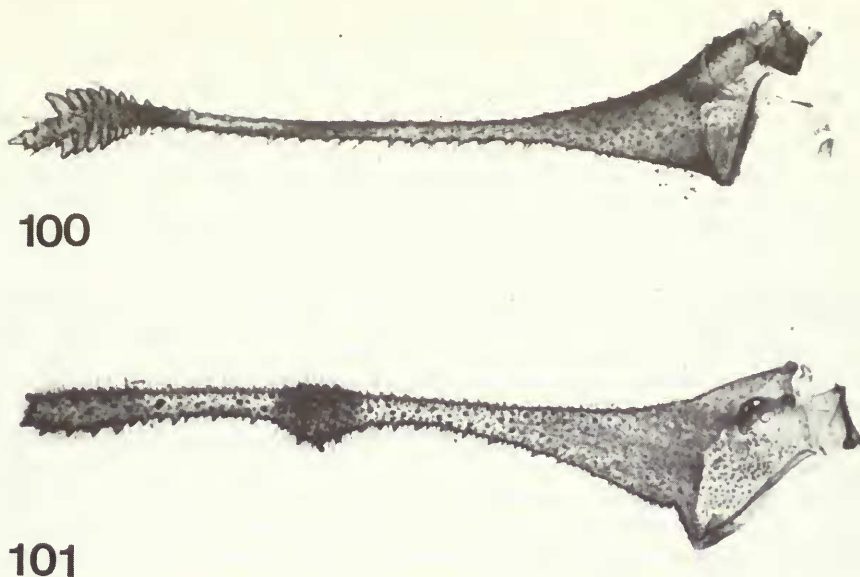
The weakly telescoped ovipositor ends in a pair of large, soft, setose, ear-like lobes (Figs 92, 93).

Juvenile stages

The shape of the egg varies within the Lepidoptera, but it is essentially flat or upright (Chapman, 1896). Many butterflies have upright eggs. In the HesperIIDae, however, they are flat. The oval egg dissected from the macerated abdomen of a female hedylid appears to be of the flat variety, but its shape did not resemble that of the hesperiid egg. Since both flat and upright eggs are found within single families, or even single genera, (Hinton, 1981), the gross shape of the egg is of limited phylogenetic significance.

The larva (Fig. 19) exhibits features of various butterfly families rather than any one of them. Its horn-like processes (Figs 19, 100, 101) strongly resemble those of many Nymphalidae. The secondary setae on the body are like those of some pierids. The crochets on the ventral prolegs of the final instar, which are arranged in a penellipse or as transverse bands, are neither like those of hesperiids (in which they form a circle) nor like papilionoids (where, in post first instars, they are usually arranged in a mesoserries). An anal comb (found in Hedylidae) is usually present in HesperIIDae and at least some Pieridae among the macrolepidopterans.

The pupa (Figs 20, 21) resembles that found in Papilionidae (see Igarashi, 1984) or Pieridae, amongst the butterflies, in that it is attached to the substrate by both a girdle and a cremaster, and that there is no cocoon. A girdle is present in some sterrhine geometrids, e.g. *Anisodes* Guenée (see Common, 1986) and *Cyclophora* Hübner. However, these genera lack the other butterfly characters discussed in the present



Figs 100, 101 Half of head capsule of larval exuviae of Hedyliidae. 100, *Macrosoma heliconiaria* (Guenée); 101, *M. nigrimacula* (Warren).

work. Furthermore, whereas the girdles of butterflies (including hedyliids) are thoracic, those of sterriine geometrids are spun around the abdomen (Holloway, pers. comm. – information derived from unpublished manuscripts housed in the British Museum (Natural History); and see Fig. 3 of Common, 1986 for an *Anisodes* girdle). The presence of a thoracic girdle is probably a ground plan character of the Rhopalocera, although weak cocoons are usually present in hesperiids. Loss of the cocoon is a typically papilionoid character, although it is present in *Parnassius* Latreille (Papilionidae) and weak and web-like in some satyrines. The girdle is present in Pieridae and Papilionidae, but is lost in Nymphalidae and many Lycaenidae.

A temporal cleavage line is said by Scott (1985) to be present in Hesperioidea, but absent from Papilionoidea. Mosher (1916) referred to the line as the epicranial suture. The apparent absence of the line in the Hedyliidae is therefore like that of true butterflies rather than that of skippers. A temporal cleavage line is found in many moths. Mosher notes its presence in Lycaenidae, although Scott (1985: table 1) records it as absent from that family.

Discussion

The Hedyliidae exhibit a high degree of structural uniformity. Several characters seem to be unique to the family, which provides evidence for its suspected monophyly. The most striking are the small chambers at the base of the fore wing, the protuberances on the underside of the hind wing, the sinuous course of veins Rs_1 and Rs_2 of the radial sector in the fore wing, and the long fore tarsi of the male composed of only two tarsomeres.

Two important questions about the phylogeny of the Hedyliidae need to be discussed. First, are hedyliids members of a taxon composed of Hesperioidea plus Papilionoidea plus themselves, i.e., are they butterflies in the broadest sense? Second, if so, what are the relationships of hedyliids, hesperiids, and papilionoids to each other: do hedyliids represent the sister group of the taxon Hesperioidea plus Papilionoidea (i.e. the Rhopalocera), or are they more closely related to the Hesperioidea or to the Papilionoidea than are either of these two related to each other? I shall argue that the Hedyliidae are indeed 'butterflies' in the broadest sense. That they may represent the sister group of the Papilionoidea remains an intriguing possibility. This possibility is not a conclusion of this work: it would be premature and requires further comparison of the three taxa involved.

A separate, but related, problem is how to treat the nomenclature. Papilionoidea and Hesperioidea are widely used names, although Hesperioidea, consisting as it does of a single family, is redundant (Farris, 1976; Wiley, 1979), assuming that the Megathyminae are not viewed as an independent family. How should the Hedyliidae be treated?

Although the butterflies are one of the best studied groups of organisms, the published evidence for their monophyly is certainly not overwhelming. Ehrlich (1958*b*) regarded hesperiids as papilionoids that retain a great many primitive characters. Both Ehrlich and Kristensen (1976) retained the two superfamilies and did not synonymize them, Ehrlich because he considered the phenetic distance between them sufficiently great, and Kristensen because he considered the sister-group relationship a reasonable working hypothesis but one that required confirmation. Although the consensus is that hesperioids and papilionoids do form a monophyletic group, the characters on which this argument is based are not entirely convincing.

Kristensen (1976) records six possible specialized characters (apomorphies) shared by the two taxa, two of which he considers doubtful. However, none of them have been examined in a great number of species of butterflies and moths. Until they are examined they must remain somewhat in doubt. A particular problem with these characters is that they are not observable on dried specimens. Some of the characters can only be seen on alcohol-preserved, or fixed material (e.g. the twist in the oblique lateral dorsal muscle of the mesothorax, and the structure of the aorta in the mesothorax). Those that can be observed on dried specimens require maceration of the head or thorax, and have been examined, inevitably, in a limited number of Lepidoptera. A detailed study of the relationships of the Hesperioidea and the Papilionoidea is being undertaken by Dr R. de Jong, who has found several specialized characters considered to support the sister-group relationship of the two taxa. If hedyliids are the sister group of papilionoids then several of de Jong's characters will have to be treated as homoplasious. It would be premature to treat the Hedyliidae as the sister group of the Papilionoidea while de Jong's detailed work is in progress. For this reason it has not been possible to make unequivocal statements about precisely which taxa some of the characters 'define'.

Recently Scott (1985) has discussed the phylogeny of the butterflies. From his table 1, the characters that appear to support the monophyly of the papilionoids and hesperioids are: the presence of a postspiracular bar, found in skippers but not in Papilionidae, some Nymphalidae, and Lycaenidae, and the presence of a secondary sternopleural sulcus, variable in size, but present in all butterflies.

No other specialized features are tabulated by Scott as unique to the adults of all butterflies, with the possible exception of the absence of spurs on the tibia of the mid leg. However, although the spurs are absent from skippers, they are lost only in Papilionidae within the true butterflies so the condition is likely to be a parallel development.

Of the attributes of the Hedyliidae described and discussed above, 13 are of particular significance in the discussion of the question of the relationship of the Hedyliidae to the skippers and true butterflies. Of these several resemble the condition in true butterflies rather than skippers.

(1). Apophyses of metathoracic furca sagittate. The sagittate condition appears to be a specialized character of the three taxa. It certainly deserves examination in many more species to establish that it is definitely absent from moths and therefore diagnostic of butterflies.

(2). Pupa girdled. Ehrlich (1958*b*) and Scott (1985) regard a girdled pupa in butterflies as primitive and its absence as specialized. Scott considers this condition to have been present in the ancestor of hesperioids and papilionoids. There is no general survey of the occurrence of girdled pupae in the Lepidoptera, so to suggest that the condition is diagnostic of hedyliids, hesperioids, and papilionoids needs to be treated with caution. This attribute derives its taxonomic strength in conjunction with others.

(3). Second median plate of fore wing lies partly under the base of vein 1A. Although this character requires examination in a wide range of Lepidoptera, it appears to support the view of the monophyly of the Hesperioidea plus the Papilionoidea (de Jong, pers. comm.) plus the Hedyliidae.

(4). Presence of an anal comb in the larva. This structure, which is present in Hesperioidea

and Hedyliidae, seems to be confined to the Pieridae in the Papilionoidea. It may reasonably be assumed to be a ground plan character of the Papilionoidea. The presence of an anal comb in the Tortricidae is probably an independent development. However, if the Macrolepidoptera are not monophyletic then the closest relatives of the Rhopalocera may be found among the microlepidopterans. The tortricoid/cossoid assemblage might be a serious contender.

(5). Presence of a postspiracular bar on the first abdominal segment. Postspiracular sclerotizations are present on the first abdominal segment of non-ditrysian moths (see for example Kyrki, 1983; Kristensen, 1984a – 'lateral lobe of tergum I' *lo* in his figure 2). That the presence of a secondary sclerotization (postspiracular bar) is a character of the ground plan of hedyliids, hesperioids, and papilionoids is a reasonable supposition. The presence of a postspiracular bar in certain Pyraloidea (those without tympanal organs), certain Geometroidea (Drepanidae, Thyatiridae, and most Uraniidae), and Noctuoidea (many families) (Brock, 1971) must cast some doubt on the value of the structure as an indicator of the monophyly of hedyliids, hesperioids, and papilionoids. The postspiracular bar is recorded as absent from macrolepidopterans by Scott (1985: table 1), although he made no comment on the postspiracular sclerotizations in the macrolepidopteran families discussed by Brock (1971).

(6). Reduction of anterior apophyses in female genitalia. The weak, reduced anterior apophyses in some Hedyliidae is a condition found also in many butterflies (de Jong, pers. comm.). Whether this is a ground plan character of hedyliids, hesperioids, and papilionoids, or whether it is one that is subject to extensive parallelism is unknown.

(7). Abdomen curved, particularly in males. As noted above, the shape of the abdomen resembles that of the true butterflies rather than that found in skippers. This character is only doubtfully a unique derivation of Hedyliidae + Papilionoidea. A detailed study, preferably measuring the degree of curvature, is needed to ascertain whether the condition in Hedyliidae and Papilionoidea is greater than that found in Hesperioidea.

(8). Abdominal tergum I strongly 'pouched'.

(9). Precoxal (paracoxal) sulcus joins 'marginopleural' sulcus. This character appears to be a specialization of the Hedyliidae and the Papilionoidea. The main objections to this view are that the sulci are difficult to observe, and that they have been examined in relatively few species.

(10). Pupal cocoon lost. Unlike the condition in hesperioids, the cocoon of hedyliids and most papilionoids is lost. Loss of a cocoon occurs elsewhere in the Lepidoptera, so this character is of doubtful value and derives its strength in consideration with others.

(11). Loss of temporal cleavage line in pupa. The loss of this cleavage line in both hedyliids and papilionoids is further, although rather weak, evidence for their close relationship.

(12). Crochets of ventral prolegs of larva not forming a complete circle. This character is based on an examination of only two species. The penellipse of *nigrimacula*, and the transverse bands of *heliconiaria* are neither the typical circle of hesperiids nor the usual mesoseries of papilionoids. It is possible, considering other characters of the family, that the hedylid condition is part of a transformation series circle → penellipse → mesoseries, but this remains a tentative suggestion.

(13). Loss of pretarsus in the fore leg of males. Reduction or loss of the pretarsus is widespread in butterflies. A reduction of the pulvilli and arolium is the condition found in all legs of the most primitive papilionoids. The initial reduction, confined as it is to the fore legs of the male, appears to be the first stage of a reduction fully established in the papilionoids. Therefore either the character is a shared specialization of the Hedyliidae plus Papilionoidea or it has developed in parallel in the two groups. The possibility remains that the pretarsus is redeveloped (a reversal) in hesperiids.

Nomenclature

The Papilionoidea are generally regarded as a separate superfamily from the Hesperioidea, although Brock (1971) combined the two in Papilionoidea. In the present study I follow convention and retain both taxa as superfamilies since the relationships between the Hesperioidea and the Papilionoidea is being studied in detail by R. de Jong. Also, Kristensen (1976) noted some uncertainties about the sister group

relationship of the two groups, and recently Stallings *et al.* (1985, quoting C. L. Remington) made a similar point.

It would be premature to formally assign the Hedyliidae to the Papilionoidea at this stage, so to retain equivalence of rank they are treated as a superfamily (Hedyloidea *stat. n.*). Consequently, the Rhopalocera now include three superfamilies Hesperioidea, Hedyloidea, and Papilionoidea, all of interchangeable position (*sedis mutabilis*, Wiley, 1979).

Epilogue: a suggested phylogeny

Although this work concluded with the conservative suggestion that hedyliids are rhopalocerans of which the precise relationships remain uncertain, the following dendrogram (Fig. 102) is a fully resolved three taxon statement presented to stimulate critical assessment.

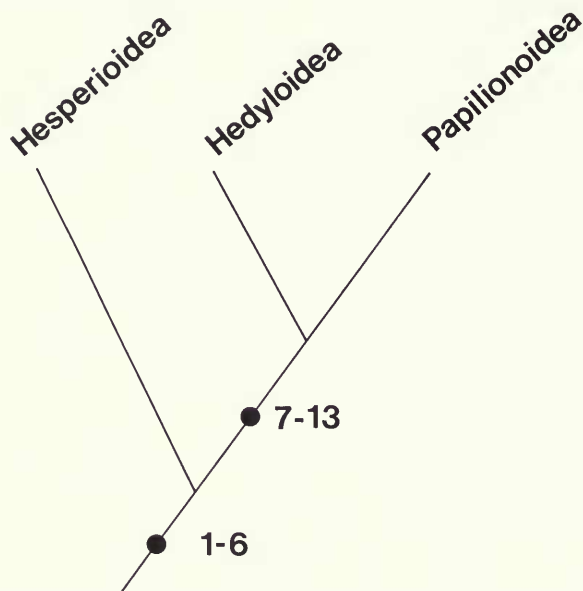


Fig. 102 Dendrogram to suggest possible phylogenetic relationships of Hesperioidea, Hedyloidea and Papilionoidea. Numbers represent the characters in the Discussion. Relative strengths and weaknesses of the characters are not indicated, but are considered in the text.

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